THE EFFECTS OF GLOBAL CLIMATE CHANGE ON LONG-DISTANCE MIGRATORY BIRDS

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THE EFFECTS OF GLOBAL CLIMATE CHANGE ON LONG-DISTANCE MIGRATORY BIRDS

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Global climate change is altering conditions across the globe. These changes are happening asynchronously among regions, creating asymmetrical changes for species whose life cycles span hemispheres. This dissertation is an attempt to use the effects of global climate change on the annual cycle of the long-distance migratory bird, the Hudsonian Godwit, *Limosa haemastica*, as a lens for understanding the broader effects of global climate change on all migratory birds. Using geolocation tracking devices and intensive breeding season studies, I show how different populations within the same species are differentially affected by climate change and how this arises because of differences in the climate change regimes experienced by the two populations, but also underlying differences in the amount of flexibility that exists in their respective annual cycles. In response to different climate change regimes, the Hudsonian Godwit populations breeding at Beluga River, Alaska and Churchill, Manitoba are altering the timing of their arrival on their breeding grounds in different ways. Beluga River godwits, which are experiencing only warming climates throughout their annual cycle, have accelerated their arrival on their breeding grounds by nearly 9 days over the past four decades. Churchill godwits, which are experiencing both warming and cooling climates, have instead retarded their arrival by more than 10 days during that same

time period. These different trends allow Beluga River godwits to remain properly timed with the period of peak insect abundance and maintain a robust breeding success rate, while Churchill godwits are instead suffering a phenological mismatch and frequent reproductive failure. Beluga River godwits are able to respond to such climatic changes because their annual cycle includes buffer events and flexibility in timing. As a result of this buffer, Beluga River godwits are able to absorb delays caused by extreme weather events that disrupt their northward migration, without suffering reductions in breeding success. Using these findings and an organism-environment approach to the whole annual cycle, I suggest that those species and populations with larger amounts of flexibility in their annual cycles can withstand significant climatic change, but that those lacking flexibility are in danger of rapidly succumbing to climatic change.

BIOGRAPHICAL SKETCH

Nathan began his life on the shores of the lovely Potomac River at George Washington Hospital in Washington D.C., but his parents, Stanley and Patricia, moved around widely during his childhood, relocating from Washington to Pennsylvania to Alaska to Colorado and then, finally, back to Alaska. It was in Alaska that Nathan found his true home and calling. At the age of eight, Nathan's father allowed Nathan to accompany him to the Copper River Delta Shorebird Festival. There on the mudflats of Hartney Bay, Nathan underwent a conversion of sorts. In the midst of tens of thousands of Western Sandpipers and Dunlin careening about in an effort to elude a hunting Merlin, Nathan fell head-over-heels in love with birds. From that point on, nothing was ever the same: birds were now the reason for Nathan's existence.

As a young teenager Nathan's parents deemed it time for him to begin striking out a bit on his own. And, so, Nathan was soon trotting off to the most remote corners of the state working as a field technician for ornithologists with the U.S. Geological Survey and U.S. Fish and Wildlife Service. Fieldwork met Nathan's need for lots of time spent watching birds and rigorous exercise, but also allowed him to gain first-hand experience working with some of the best field biologists in the world. Two of these, Mr. Robert Gill and Dr. Colleen Handel, would provide Nathan with tremendous mentorship and become long-lasting colleagues.

Upon graduating from high school, Nathan dispersed slightly southward to central Minnesota and Carleton College. At Carleton, Nathan spent considerably more time in the arboretum watching birds and running for the cross-country team than he did thinking about classes. Thankfully he passed enough muster to be able to

participate in field courses that spent winters in Costa Rica, Ecuador, and the Galapagos. On those courses, under the tremendous guidance of professors Mark McKone and Matt Rand, Nathan began to more fully comprehend the complexity of biology and develop a taste for the great continent of South America, something that would serve him well in his next endeavor.

During his senior year at Carleton, Nathan, as with most seniors, couldn't make up his mind about what he wanted to do with his soon-to-be-had freedom. He knew it had to involve birds, he really wanted it to involve travel in South America, and he knew it had to be paid for by someone else. On something of a lark, he decided to apply for a Thomas J. Watson Fellowship, which provides graduating seniors nationally the funding to pursue the research project of their choice outside of the United States for one full year. With the help of Professor Roy Grow, Nathan crafted a project that would prove fortuitous for his future life: He decided to try to unravel the mystery of the migration of Hudsonian Godwits. While people knew where godwits bred — Arctic and sub-arctic Alaska and Canada — and knew where they spent the winter — the very southern tip of South America — no one quite knew how they traveled in between those two places. Nathan believed that with enough time and the right hitchhiking skills, he might just able to solve the mystery. To Nathan's surprise and considerable consternation, the Watson Foundation agreed with him and awarded him a fellowship, and so he was required to actually follow through with what he had proposed.

What ensued was the most amazing year anyone could imagine. Nathan traveled the length of the Western Hemisphere, touching down in eight countries —

Canada, Mexico, Panama, Peru, Chile, Argentina, Uruguay, and Brazil — and took more overnight buses and ate more dry bread and cold cheese then he would ever care to think about again. He also laid the foundation for his dissertation work; on the shore of Bahía Bustamante in Patagonian Argentina, Nathan developed the seed of what would eventually become his PhD project.

Upon returning to the U.S., Nathan took up residence in Oregon, worked construction, ran as much as possible, and took environmental consulting jobs when he could. In summer he traveled back to Alaska to work field jobs and keep his hand in Alaskan ornithology. Then, in the fall of 2006, he received a fateful phone call from his old mentor, Robert Gill. Bob called to tell Nathan that he and another colleague, Nils Warnock, had just received a substantial grant from the David and Lucile Packard Foundation to fund a large-scale tracking study of shorebirds in the Pacific Basin and that one of the focal species would be Hudsonian Godwits. Nathan couldn't quite believe his ears and somehow had the nerve to ask right then and there if they needed someone to head up the Hudsonian Godwit work. Bob, even more surprisingly, said that, in fact, they did need someone to work with godwits. Thus was born Nathan's life at Cornell.

At Cornell, Nathan has enjoyed the incomparable community to be found in the Ecology and Evolutionary Biology department and at the Cornell Lab of Ornithology. Under the guidance of Dr. John Fitzpatrick, Nathan has been able to make the dream he had in Bahía Bustamante become a reality: He has helped solve the mystery of Hudsonian Godwit migration and also extended his work to focus on how climate change is disrupting the annual cycles of long-distance migratory birds. He has

also been able to take on fulfilling side projects, such as the Peruvian Shorebird Atlas with colleague Fernando Angulo, and the Arctic Shorebird Demography Network with Drs. Brett Sandercock, Stephen Brown, and Richard Lanctot. And he has worked with the Cornell Lab Mutlimedia and Education departments to create outreach projects that spread information and interest about migratory birds.

Now Nathan is off to the green meadows of the Netherlands and the University of Groningen. In the Netherlands, he will work with shorebird guru Dr. Theunis Piersma on the migration and conservation of Black-tailed Godwits, the second coolest bird in the world.

To my parents, Patricia and Stanley, for instilling in me a love of life, exploration, and stewardship of the natural world.

ACKNOWLEDGMENTS

Having the opportunity to undertake this project has truly been a dream come true. When I was sitting and watching Hudsonian Godwits and Red Knots forage on the mudflats of Bahía Bustamante, I came up with a project that I thought I might one day undertake as the culmination of a long career. Instead I was able to make it my dissertation project. Some days I still do not really believe how lucky I am for that. And, so, I want to begin by thanking Mr. Robert Gill of the U.S. Geological Survey and Dr. Nils Warnock of Audubon Alaska. Without their willingness to put the success, in part, of their Pacific Shorebird Migration Project in the hands of an untested, soon-to-be graduate student, this dream would not have come true. For that and for their friendship, their mentorship, and their long-term collaboration, I am immensely appreciative.

I also cannot go any further without thanking my advisor Dr. John Fitzpatrick. My project was not a small one and I am sure that there were more than a few times when Fitz wondered whether it was worth it for the Cornell Lab of Ornithology to be investing so much in one graduate student and one dissertation project. I hope that he still believes that the investment was worth it. I can definitively say that I would not have been able to undertake this project, or have succeeded in undertaking this project, with any other advisor. I have the utmost respect for Fitz and all that he has done for the Cornell Lab, for science, and for the conservation of birds, beyond his mentorship and support of me. I am so thankful that I was able to spend the past five years working with him.

To the rest of my Cornell committee, thank you for your patience, your

willingness to understand my peregrinations around the globe and my constant pounding of the streets and trails of Tompkins County while training for marathons, and your attention and interest in my work. Dr. David Winkler, your lab group provided me a home and gave me some of the most fun and intellectually stimulating conversations that I have had anywhere. You were also a huge part of why I wanted to come to Cornell and critical for making sure that I was able to succeed once I got here. Dr. Walter Koenig, you always brought a new perspective to my work and kept me from getting a little too pigeon-holed into my world of shorebird migration. Thanks to both of you.

Thank you also to my "shadow committee." Dr. Theunis Piersma, you have provided so much inspiration and so much insight. I cannot wait for the next few years when we are able to work together, not separated by an ocean. Dr. Wesley Hochachka, your statistical aptitude and perennial good cheer have been such a boon these past few years. Drs. David Douglas, Brett Sandercock, Brad Andres, Colleen Handel, Richard Lanctot, Stephen Brown, and Eldar Rakhimberdiev; Misters Dan Ruthrauff, Jim Johnson, Fernando Angulo, Jorge Valenzuela, Luis Espinosa, Fabrice Schmidt, Thomas Valqui, Richard Johnston, and Alex More; and Ms. Nataly Aranzamendi, Lee Tibbitts, and River Gates, your collaborations have been a huge help and I look forward to continuing them in the future. It has been a pleasure working with you.

In some ways, my biggest thanks of all goes to the many, many field assistants that have helped me over the past five years — William Abbott, Amy Alstad, Hope Batcheller, Shawn Billerman, Jon DeCoste, Doug Gochfeld, Mike Harvey, Mike Hilchey, Tom Johnson, Andy Johnson, Julia Karagicheva, Jess Marion, Madi

McConnell, Jay McGowan, Brittany Schultz, Glenn Seeholzer, Hannah Specht, and Brad Walker. You all have been like family to me and I greatly appreciate the blood (thank you mosquitoes and black flies), sweat, and miles that you put in for this project. I wish that I could have paid all of you so much more. Hopefully the experiences were worth it nonetheless.

To the administrative staff at the Cornell Lab of Ornithology and on campus in Ecology and Evolutionary Biology, I owe you a tremendous debt of gratitude. Thank you for all of your efforts in helping me to navigate the ins and outs of many, many grants and the complex Cornell bureaucracy. I especially appreciate the efforts of Cindy Marquis, Jennifer Harris, Myrah Bridwell, Melissa Switzer, Theresa Griffin, Patricia Jordan, Carol Damm, Janeen Orr, and Debra Dolittle. Thank you also to Cheri Gratto-Trevor, John Pearce, and Jon Dunlop in Canada and Alaska for their bureaucratic help as well. You can all now breathe a huge sigh of relief because I am finally done and you won't have to put up with me anymore!

In Beluga, Judy and Larry Heilman and Clarke and Becky Smith have made my time there a happy one; the staff at ConocoPhillips has made it a smooth one. In Churchill, the people at the Churchill Northern Studies Centre have made their research station a home away from home. Thanks especially to LeeAnn Fishback and Carley Basler for all of their help.

Despite this project being a dream come true, my time at Cornell has not always been easy. There are some times that I wish I could forget and things that I wish could have turned out otherwise. But one of the reasons that I most wanted to come to Cornell was because the community I met here during my interview weekend

was so warm and welcoming that I knew it was the right place for me. Little did I know that I would have to make such extensive use of that community, but I am so glad that I did. Quinn Thomas, Cayelan Carey, Chris Wood, Jessie Barry, Maria Stager, and Tom and Michi Schulenberg, you have provided me with the stability and support that I needed when I needed it most. I hope that in some way I can repay all of you one day. Jimmy O'Dea, Jon Lambert, Ian Golden, Petra Deane, Anna Forsman, Scott Callan, Loretta Bennett, Dave Cerasale, Ben Freeman, Alexa Class, Carolyn Sedgwick, Tim Lenz, Eric Liner, Nancy Chen, Jeff Gerbracht, and Charles and Erin Eldermire, thank you all for your friendship and support. You have been unbelievably good to me.

To Kate, this project would never even have been a glimmer in my eye without you.

And to my parents, Patricia and Stanley, and brothers, Paul and Daniel: What more can I really say? I am not sure how many parents would have let their 14 year old son wander off to work amongst polar and grizzly bears in some of the most remote corners of Alaska; I am not sure that I would have. I am so appreciative that you did. That decision has changed so much about my life and made so much possible for me, and not just because I found scientists to mentor me or opportunities to take me to amazing places, but because I gained the confidence to move about in the world and the experience to work through tough times. Thank you also for your love and unstinting support in all that I have done, I couldn't ask for anything more.

Finally, I am incredibly grateful for all of the generous donors who supported my research. For that, thank you to the David and Lucile Packard Foundation, U.S.

Fish and Wildlife Service, Faucett Family Foundation, National Science Foundation, Cornell Lab of Ornithology, the Atkinson Sustainable Biodiversity Fund at Cornell University, Cornell Graduate School Mellon Fund, Cornell Chapter of Sigma Xi, American Museum of Natural History, Ducks Unlimited Canada, Churchill Northern Studies Centre, American Ornithologists' Union, and Arctic Audubon Society.

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PREFACE

This project began as an attempt to solve a mystery involving a single species and evolved into an attempt to document and understand the consequences of a burgeoning ecological crisis for an entire class of organisms. This shifted the focus of the project from simply documenting and quantifying the life-history of one long-distance migratory bird species, to using that species as a lens for viewing the effects of global climate change on all long-distance migratory birds. Widening the scope of the project also broadened its perspective on the ecology and evolution of long-distance migratory birds and what facets of their life-history must be considered important for gaining a fuller understanding of their future in a world of rapid environmental change. Ultimately, global climate change is unique only in the diversity of its potential effects, not in the evolutionary and ecological forces that it brings to bear on species and ecosystems.

In its final form, then, this project encompassed a number of disparate worlds and had to consider the influences of physiology, food-web ecology, meteorology and climatology, demography, and landscape ecology, all in an attempt to comprehensively view the myriad factors potentially influencing a species' ability to respond to rapid environmental change. In order to make sense of this multitude of influences, the project relied upon a variety of data sources — geolocation tracking devices, radio telemetry, historical arrival data, chick growth rates, insect pitfall traps, and global-scale climate and weather data — and a suite of powerful analytical tools — mark-recapture analysis, non-linear mixed effect models, multi-stage generalized linear models, and dynamic programming.

As its basis, this project focused on one species — the Hudsonian Godwit, *Limosa haemastica* — and its migration from the southern tip of South America to the Arctic and sub-arctic of Alaska and Canada to help explain the broader changes taking place that affect long-

distance migratory birds. In the end, this one species provided an effective lens because its life cycle is so dramatic that godwits embody many of the risk-factors associated with susceptibility to climate change; its physiology so impressive that it undergoes enough changes during the course of its annual cycle to encompass a significant proportion of the physiological variety found in the rest of the bird world; and its migration so epic it brings godwits in contact with many of the regions of the globe most affected by climate change. Thus, to provide an introduction to a dissertation about Hudsonian Godwits and climate change, we must discuss Hudsonian Godwits and climate change.

Hudsonian Godwits can be divided into three largely separate populations: One population breeds in southcentral and western Alaska and spends the boreal winter on Isla Chiloé and the adjacent mainland of southern Chile. Another population breeds in the Arctic of northeastern Alaska and northwestern Canada and likely winters along the coast of northern Argentina. The third population breeds along the western shore of Hudson Bay and winters on Tierra del Fuego and the southern coast of Patagonian Argentina (Walker et al. 2011).

The Arctic and sub-arctic exhibit some of the most rapid climatic change on the globe and are projected to change more significantly than all other biomes (IPCC 2007). These rapid and dramatic changes have already altered the short Arctic and sub-arctic summers to a significant degree and begun affecting the ability of sub-arctic and Arctic-breeding species, such as Hudsonian Godwits, to properly time their breeding efforts with peaks in local resource phenology (Schekkerman et al. 2003). Chapter 1 concerns how two Hudsonian Godwit populations — southcentral Alaska and Hudson Bay —are altering the timing of their arrival at their breeding sites in response to these phenological changes. Chapter 2 addresses what the effects of these phenological changes are on the breeding success of these two godwit

populations.

After the rapid breeding season, godwits move southward to staging sites (Warnock 2010) and then, using multi-day, non-stop flights, migrate onto their wintering areas in southern South America. In order to complete this migration and arrive at their non-breeding sites, godwits must first fully recover from the breeding season and undergo a physiological transformation that likely involves doubling or tripling their body mass, tripling the size of their flight muscles, diminishing their digestive organs two-to-seven fold, and increasing their fat stores 150-fold (Piersma et al. 1993, Piersma et al. 1999, Piersma et al. 2005, Dietz et al. 2007). Then, they must survive tropical storms and flights of up to seven days and 10,000 km before arriving at their destinations. Climatic changes in the Prairie Provinces of Canada are threatening the staging areas where these physiological transformations take place (Johnson et al. 2010), while the increased frequency and strength of North Atlantic hurricanes threaten their migratory flights (Villarini and Vecchi 2012). To understand how godwits are currently coping with these stresses and to understand how stresses are accrued and dissipated throughout their entire annual cycle, Chapter 3 explores whether carry-over effects impinge on the timing of the godwit annual cycle.

During the non-breeding season, godwits remain largely stationary while making use of large intertidal mudflats in secluded bays dotting the Southern Cone of South America. While there, they must recover from their southward migration, undergo two separate molts, and prepare for their northward migration and breeding season.

After this period of comparative rest, godwits once again embark on long, non-stop flights moving northward, this time with the added necessity to properly time their arrival with environmental conditions favorable for breeding and raising young (Alerstam 2006). Given their

need to move rapidly along their 15,000 km migratory route, climatic changes, such as increased storm incidence or altered wind regimes, can significantly affect the timing and success of godwit northward migration. Chapter 4 documents how stochastic weather events and habitat availability alter godwit migration and, ultimately, affect their arrival on the breeding grounds and breeding success.

Chapter 5 encapsulates the findings of the first four chapters and uses them to create a framework for understanding how global climate change will affect other migratory bird species. This chapter takes an organism-environment approach (Wingfield et al. 2011) to the godwit annual cycle and proposes how an in-depth understanding of the constraints acting on an annual cycle, and how those constraints affect a species' flexibility, are critical to understanding how climate change will influence the future trajectories of long-distance migrants.

Overall, this project moves with godwits from the breeding season to their staging areas, through their southward migration, non-breeding season, and northward migration, back to the Arctic again, and it scales from the phenological to the global. Such a scope ultimately may be necessary to understand fully the interactions between global climate change and any organism, not just a long-distance migratory bird.

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CHAPTER 1

ONE SPECIES BUT TWO PATTERNS: POPULATIONS OF THE HUDSONIAN GODWIT (*LIMOSA HAEMASTICA*) DIFFER IN SPRING MIGRATION TIMING

ABSTRACT

Climate change can cause mismatches between the breeding phenology and peak abundance of food resources of migratory species. Moreover, asynchronously changing climate regimes across their ranges may constrain the ability of migratory species to adapt to all the regimes they encounter. To understand the potential effect of asynchronous changes, I examined the influences of both large- and local-scale weather and climate on the timing of arrival of two disjunct breeding populations of Hudsonian Godwits (*Limosa haemastica*). I used arrival data from two study sites—Beluga River, Alaska, and Churchill, Manitoba—combined with 37 years of weather and climate data from both winter and stopover sites and the breeding grounds. The Alaskan population now arrives ~9 days earlier than it did in the early 1970s, and the Churchill population arrives >10 days later. A model-selection process using linear regression models suggested that these divergent trends result from different suites of environmental factors affecting the timing of migration for the two populations. The cues used by the Alaskan population have remained reliable indicators of the timing of the onset of spring on their breeding grounds, but this is not the case for the Churchill population. Conflicting warming regimes in midcontinental North America cause the Churchill population to arrive later to their breeding grounds and limit their ability to properly time their breeding efforts. These results suggest that ecological and phenological limitations, not just evolutionary constraints, are critical

to determining how populations respond to climate change.

INTRODUCTION

Global climate change is altering ecosystems around the world (Root et al. 2003). Regional and local manifestations of climate change mean that some areas are changing faster than others, with Arctic and sub-Arctic regions warming faster than the rest of the earth (Serreze et al. 2000, Intergovernmental Panel on Climate Change 2007). Rapid climate change in the Arctic (Wang et al. 2009) presents ecological and evolutionary hurdles to organisms across trophic levels (Parmesan 2006) but may be especially challenging for Arctic-breeding organisms that regularly migrate long distances (Batalden et al. 2007, Vors and Boyce 2009).

To properly time events such as breeding and molt that occur in geographically disparate locations, migratory species must integrate information from across a range of both spatial and temporal scales (Frederiksen et al. 2004, Gill et al. 2009). Because the rate of climate change can differ dramatically across regions, migrant species frequently encounter asynchronously changing climate regimes during the course of their annual cycle (Ahola et al. 2004, Fontaine et al. 2009). As a consequence, migrants may be unable to reconcile these different rates of change; they may properly track one set of cues, but simultaneously fail to successfully time events occurring in a location with a different climate-change regime (Strode 2003, Both 2010). Long-distance migratory species that must closely track local resource phenology on their breeding grounds to successfully reproduce may be particularly susceptible to such climate-driven mismatches because of the greater number of climate-change regimes that they have to reconcile (Both and te Marvelde 2007, Jones and Cresswell 2010). Mismatches are already known to compromise breeding success in numerous taxa, including both long-distance migratory birds

(Both and Visser 2001) and ungulates (Post and Forchhammer 2008), leading to large-scale population declines (Both et al. 2005, Vors and Boyce 2009, Jones and Cresswell 2010).

In seeking to understand the cause of phenological mismatches in migratory birds, numerous studies have focused on the migratory period preceding birds' arrival on their breeding grounds (reviewed by Dunn and Winkler 2010). These studies have revealed that large-scale climatic fluctuations or events that occur outside of the migratory period explain much of the inter-annual variation in arrival times for some species (Hüppop and Hüppop 2003, Gordo et al. 2005). Marra et al. (2005) and Van Buskirk et al. (2009) have also suggested that many species, even if closely related, may differ in their responses to climate change. However, many of these studies have focused solely on large-scale patterns and multispecies assemblages (Van Buskirk et al. 2009). This approach may be too coarse to identify the cues relied upon by individual populations to time their annual cycles (Frederiksen et al. 2004, Hüppop and Winkel 2006). These studies may also fail to distinguish between phenological mismatches that result from an inability to adapt to phenological changes and mismatches for which adaptation is impossible (Strode 2003, Both 2010). The logical next step is to explore responses to simultaneous changes in climate that occur at multiple scales, and to incorporate the effects of both local-scale weather events and global phenomena to search for intra- as well as interspecific differences in the responses of migrants to climate change (Hüppop and Winkel 2006, Gienapp et al. 2010, Robson and Barriocanal 2011).

Here, I explore how both local-scale weather conditions and larger-scale climate drivers affect the timing of migration of two widely separated breeding populations of a long-distance migratory bird, the Hudsonian Godwit (*Limosa haemastica*; hereafter "godwit"). On the basis of qualitatively different migration strategies, I hypothesized that the two populations are

responding differently to climate change because the timing of their spring arrivals depends on different cues, which are appropriate to the respective geographic and climatic settings of their migratory bottlenecks (here defined as periods during which some aspect of a bird's biology is significantly taxed, such as preparation for a long, nonstop flight). My objectives were (1) to identify whether the two populations use the same or different cues to determine timing of arrival on their nesting grounds and (2) to determine whether the differences in apparent responses to climate change could be overcome through adaptation or are the result of irreconcilable changes in migratory cues and constraints.

METHODS

Study Species

Godwits are a species of high conservation concern because of their small, but apparently stable, population size and the existence of threats throughout their range (Senner 2010). Godwits migrate from southern South America to Arctic and sub-Arctic Alaska and Canada and are presumed to employ an elliptical migration route that leads them south from their breeding grounds via the Atlantic Flyway to their wintering grounds and then back north via the Pacific and Central flyways (Morrison 1984). Because of the relative paucity of fall records along the Atlantic coast of North America and spring records anywhere away from their main wintering sites in South America, they are also thought to employ long, nonstop flights, akin to those exhibited by Bar-tailed Godwits (*L. lapponica baueri*) and other migratory shorebirds (Piersma 1987, Gill et al. 2009). On the breeding grounds, the species is divided into three disjunct populations—Hudson Bay, the northern Northwest Territories and northeastern Alaska, and south-central and western Alaska (Walker et al. 2011). During winter the populations separate

into three corresponding wintering populations in Argentina and Chile: (1) bahías Lomas and San Sebastián on Tierra del Fuego; (2) Bahía Samborombón in northern Argentina; and (3) Isla Chiloé and the adjacent Chilean mainland (Morrison and Ross 1989, N. R. Senner unpubl. data).

Phenology differs among godwit breeding and wintering areas, but especially among breeding sites (Walker et al. 2011). Arrival dates at breeding areas span ~1 month. Godwits arrive in south-central Alaska during the last week of April and first week of May, but at Hudson Bay and Northwest Territories they arrive during the last week of May and first week of June (Walker et al. 2011). As a result, northbound migration is also likely offset among the populations. Records from the Avian Knowledge Network (hereafter AKN; see Acknowledgments) suggest that both time and space isolate the migrations of the two populations that I study. The first wave of godwits arrives on the Gulf of Mexico coast in early April, and ~3 weeks later a second pulse arrives in late April and early May. Presumably, the first wave represents the Alaskan birds and the second the Hudson Bay birds.

Once on the breeding grounds, clutches are largely complete within 10 days of arrival (N. R. Senner and B. K. Sandercock unpubl. data). Incubation lasts ~22 days and the chick period ~30 days, at which point adult godwits leave the breeding grounds, likely for staging areas farther south (Walker et al. 2011). In total, adult godwits are on the breeding grounds for ≤70 days (N. R. Senner unpubl. data).

Datasets

I studied two godwit populations, one at Beluga River, Alaska (61°21′N, 151°03′W), in 2009–2010 and one at Churchill, Manitoba (58°93′N, 93°80′W), in 2008–2010. The two sites correspond roughly to the center of the breeding range of each population and allowed me to link my own data with historical arrival dates at these sites (1974–2008; R. L. Scher and R. Rockwell

unpubl. data). First-arrival dates can be misleading (Tryjanowski and Sparks 2001, Tøttrup et al. 2006), but Arctic breeders typically have relatively synchronous arrivals (Smith et al. 2010). I found that all marked individuals in my populations arrived within a 5-day window, making use of first-arrival dates appropriate for the present study (N. R. Senner unpubl. data).

On the basis of differences in arrival dates on the breeding grounds and on a significant gap between the two waves of godwits appearing in the midcontinental U.S. (Walker et al. 2011), I define the period of passage as 5–25 April for Alaskan godwits and 5–25 May for Churchill godwits. To describe conditions faced during migration of each population, I used April weather conditions for Alaskan godwits and May conditions for Churchill godwits.

Because godwits are midcontinental migrants in spring and do not consistently use specific stopover sites, I identified important regions, rather than specific sites, used during their northward migration, using data from the AKN and reports of concentrations from the 37-year study period (Figure 1.1; Skagen et al. 2008, Senner 2010). Because AKN records suggest that Hudson Bay godwits stop more frequently, I identified a larger number of stopover regions for them than for Alaskan godwits (Figure 1.1). Wintering areas were identified from historical aerial surveys combined with resightings of banded godwits marked at Beluga River and Churchill. Resighting efforts were carried out during annual shorebird-related field work on Isla Chiloé and Tierra del Fuego, but also by volunteer observers throughout both Argentina and Chile. These efforts found that Alaskan godwits winter almost entirely on Isla Chiloé (28 of 30 resightings), whereas Churchill godwits winter largely on Tierra del Fuego (7 of 9 resightings; N. R. Senner unpubl. data).

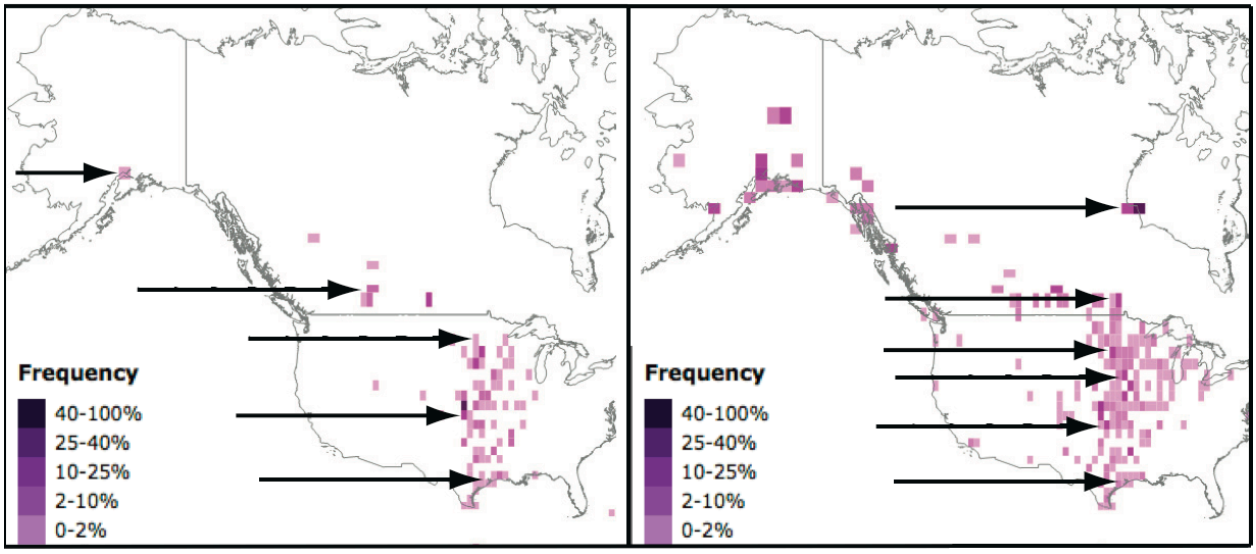

FIGURE 1.1: Occurrence of Hudsonian Godwits during spring migration through midcontinental North America. (A) Occurrences during the period 5–25 April, when the south-central Alaska population is presumed to migrate through this corridor; and (B) occurrences during the period 5–25 May, when the Hudson Bay breeding population is presumed to migrate through this corridor. Important regions (and cities) from which weather and climate data were chosen (on the basis of concentrations of observations) are denoted with arrows. For Alaskan Hudsonian Godwits (from south to north), those regions are the Gulf Coast of Texas and Louisiana; the southern Great Plains of Oklahoma, Kansas, and southern Nebraska; the central Great Plains of South Dakota, North Dakota, and western Minnesota; and the northern Great Plains of Saskatchewan and Alberta. For Churchill Hudsonian Godwits, those regions are the Gulf Coast of Texas and Louisiana; the southern Great Plains of Oklahoma and southern Kansas; the Rainwater Basin and Missouri River Valley of Nebraska and Iowa; the central Great Plains of South Dakota, North Dakota, and western Minnesota; and the northern Great Plains of Saskatchewan and Manitoba. Maps were created using eBird data (see Acknowledgments).

To characterize weather in these regions during winter and migration, I chose cities corresponding to the centers of each region—Puerto Montt, Chile; Houston, Texas; Wichita, Kansas; Fargo, North Dakota; and Saskatoon, Saskatchewan for Alaskan godwits; and Rio Grande, Argentina; Houston, Texas; Oklahoma City, Oklahoma; Omaha, Nebraska; Sioux Falls, South Dakota; and Winnipeg, Manitoba for Churchill godwits—from which to obtain meteorological data (National Climatic Data Center; see Acknowledgments). I also obtained large-scale climatic data—the North Atlantic Oscillation (NAO) and Southern Oscillation Index (SOI)—that describe general weather variation that potentially influences the godwit annual cycle (Earth System Research Laboratory; see Acknowledgments).

Selecting Predictors of Migration Timing

I used first-arrival dates from 1974–2010 for Beluga River, Alaska, and from 1974–1994 and 2008–2010 for Churchill, Manitoba, to document arrival of godwits on breeding territories. Data for the Beluga River population from 1974–2008 were collected nearby (within 50 km) in Anchorage, Alaska, using daily surveys of the city's 2-mile stretch of intertidal mudflats (R. L. Scher unpubl. data); in 2009–2010, I collected data both in Anchorage and at Beluga River and found no differences. Biologists collected data for the Churchill population from 1974 to 1994 at the nearby (within 30 km) La Pérouse Bay field station as part of their daily observations (R. Rockwell unpubl. data); I collected data in 2008–2010 at godwit breeding sites in Churchill. Effort was not calculated but did not vary substantially among years (R. Rockwell and R. L. Scher pers. comm.).

Recent work has highlighted the ability of local weather events to determine the speed with which species migrate, especially through its effect on departure decisions and the duration of long flights (Gill et al. 2009). As indices of the potential influence of local-scale weather

conditions on migration, for each city I chose the three variables most frequently cited as having effects on migration timing and duration: mean temperature, total precipitation, and mean wind speed (Åkesson and Hedenström 2000, Schaub et al. 2004, van der Graaf et al. 2006). These weather variables have the potential to alter migration progress by causing the amelioration or deterioration of conditions at stopover sites (temperatures, rain) or during flights (wind, rain).

In all cases, measurements were made using ground-based instruments (National Climatic Data Center), which were the only data available for the full duration of the present study. Although previous studies have identified that winds from higher altitudes were the best correlates of shorebird stopover behavior, ground-based winds were significantly correlated with stopover decisions and are appropriate for the present study (Ma et al. 2011). Wind direction can influence the effects of wind on migration (Sinelschikova et al. 2007, Gill et al. 2009), but data on daily wind direction are available only from a few sites and only during recent years. Some studies have also found that wind speed is a more important predictor of departure conditions than wind direction (Schaub et al. 2004).

I used the same variables as during the migration period, averaged over the duration of the non-breeding season, at the wintering areas to account for any effects of non-breeding-season weather on the timing of migration (Gordo et al. 2005). On the non-breeding grounds, wind, precipitation, and temperature probably have a narrower array of effects than they do during the migration period. Because both populations winter in the south temperate and sub-Antarctic zones, conditions causing warmer temperatures, less wind, and less rain likely benefit overwintering godwits by minimizing self-maintenance costs (Piersma 2002). During the departure period, however, wind may aid or hinder departure, depending on its direction (Åkesson and Hedenström 2000).

I used an expanded suite of variables from both breeding sites—including variables from the most recent and preceding winters as well as from each spring month prior to arrival (Findlay and Cooke 1982, Gaston et al. 2005, Smith et al. 2010)—to account for the potential effects of conditions on the breeding grounds in determining arrival dates. (Because Beluga River lacks a permanent weather station, I used nearby Anchorage as its proxy.) Each predictor variable provides information on the timing of spring, which has a strong influence on breeding success and, as such, may act as a driver of selection for arrival timing (Durant et al. 2004).

Finally, I also used long-term records of the NAO and SOI—in both cases, the index value averaged over the entire non-breeding season and the value from each month of that period (Hüppop and Hüppop 2003, Wolfe and Ralph 2009). The SOI can affect rainfall, the strength and persistence of trade winds, and the strength of storm tracks in the Pacific Basin (Ropelewski and Halpert 1996, Harrison and Larkin 1998, Renault et al. 2009). These changes can affect conditions for godwits, especially during their northward migration, which is presumed to rely strongly on the consistent winds of the Humboldt Current (Morrison 1984). The NAO can have a similar effect on much of continental North America, altering precipitation and wind patterns and affecting ice build-up and the timing of spring in the Arctic (Hurrell et al. 2001, Gagnon and Gough 2005a).

Building the Set of Candidate Models

To identify which portion of the migration corridor was most important to each population, I created a series of competing models based on hypotheses already present in the literature. I identified six non-mutually-exclusive hypotheses that could explain either the timing of a species' arrival on its breeding grounds or duration of its migration. (1) Prior cue use: Godwits use cues from the previous year on their breeding grounds to time their current year's arrival,

either because their circannual rhythms are set by that cue or because that cue is the best predictor of future events (Durant et al. 2004). (2) Current conditions: Godwits use the current conditions on their breeding grounds to time their arrival, by staging close enough to the area to determine when conditions are amenable to breeding (Findlay and Cooke 1982). (3) Large-scale climate: Godwits use large-scale climatic factors to time their arrival, because these factors can affect weather throughout large swaths of their migration corridor (Hüppop and Hüppop 2003). (4) Local conditions: Godwits use local conditions—which may be affected by large-scale climate drivers, but also by local topography and competing regional weather systems—along the migration corridor to time their arrival, either by speeding up or slowing down their migration as they assess conditions at each stopover site (Robson and Barriocanal 2011). (5) Non-breeding conditions: Conditions on their wintering grounds determine when godwits depart on migration, through effects on premigratory fattening and molt (Gordo et al. 2005). (6) Bottlenecks: Godwits use conditions occurring at "bottlenecks" during their annual cycle to time their arrival on the breeding grounds (Buehler and Piersma 2008).

Bottlenecks are periods during which some aspect of a bird's biology is significantly taxed and were identified subjectively following Myers (1983) and Buehler and Piersma (2008). Buehler and Piersma (2008) identified four different types of bottlenecks—nutritional, energetic, temporal, and disease risk—whereas Myers (1983) identified a fifth, ecological, to encompass those areas at which large concentrations of birds congregated either directly before or after a long, nonstop flight. Documentation of all bottlenecks that could affect a population requires a deep understanding of the population's entire ecology, something that is not yet possible for godwits (Senner 2010). For the present study, I identified three potential bottlenecks along the migratory route of each population that I judged as combining key characteristics of the five

types of bottlenecks. For each population, the set of three bottlenecks included one each of non-breeding sites (because these are often nutritional and energetic bottlenecks) and breeding sites (energetic and temporal bottlenecks) and, third, a stopover or staging site in the middle of the migration corridor (nutritional, temporal, and ecological bottlenecks). In the case of the Alaska population, I considered Puerto Montt, Houston, and Anchorage possible bottlenecks. For the Hudson Bay population, I considered Rio Grande, Omaha, and Churchill possible bottlenecks. Houston and Omaha were chosen because those regions produced the highest counts from each population's period of passage (AKN, Senner 2010).

Analysis

Given that arrival dates for the two populations could be affected by different climatic features, and given the large number of models required to simultaneously identify the relevant climate variables for each population and compare between the populations, I broke my analyses into two stages. In the first stage, I identified the best-supported predictors of arrival date for each population separately. In the second stage, I examined whether the same climate features affected migration timing in both populations. All statistical analyses were done in the R statistical package (R Development Core Team 2009), using the "bbmle" and "MuMIn" libraries and the "lm" function.

Prior to the first stage, I pared down the set of predictors from 59 (3 predictors per stopover site, 6 per wintering site, 6 per breeding site, and 4 per large-scale climatic variable) to 21 to eliminate multicollinearity, using Pearson correlations to identify pairs of variables with significant collinearity ($P < 0.05$), and eliminated one of each such pair, keeping whichever was more highly correlated with godwit arrival date for the final model analysis (Table 1.1). I then separately tested among each population's competing models using linear regression models and

TABLE 1.1: Variables included in final model-selection analysis for populations of Hudsonian Godwits breeding at Beluga River, Alaska, and Churchill, Manitoba.

Beluga River	**Churchill**
Anchorage 5-year mean arrival-period temperature (Anc_5yr)	Churchill mean arrival-period temperature (Chu_Arr_Temp)
Anchorage current year's mean arrival-period temperature (Anc_Arr_Temp)	Churchill 5-year mean arrival-period temperature (Chu_5yr)
Anchorage previous mean arrival-period temperature (Anc_Prev_Arr)	Churchill previous year's mean arrival-period temperature (Chu_Prev_Arr)
Anchorage previous year's total snowfall (Anc_Prev_Tot)	Churchill mean annual temperature (Chu_Ann_Temp)
Anchorage total snowfall (Anc_Tot_Snow)	Churchill previous year's mean breeding season temp. (Chu_Prev_Bre)
Anchorage 5-year mean total snowfall (Anc_5yr_Snow)	Rio Grande mean temperature winter (RG_Mean_Temp)
Anchorage current year's arrival-period snowfall (Anc_Arr_Snow)	Rio Grande, Arg. number of winter rainy days (RG_Rainy_Days)
Saskatoon total passage-period precipitation (Sas_Pas_Prec)	Rio Grande mean departure-period wind speed (RG_Apr_Wind)
Saskatoon mean passage-period temperature (Sas_Pas_Temp)	Houston mean passage-period temperature (Hou_Mean_Pas)
Puerto Montt mean temperature, winter (PMC_Mean_Temp)	Houston mean passage-period wind speed (Hou_Pas_Wind)
Puerto Montt precipitation, winter	Houston total passage-period precipitation

Beluga River	**Churchill**
(PMC_Precip)	(Hou_Pas_Prec)
Puerto Montt mean departure-period wind speed (PMC_Dep_Wind)	Departure-period Southern Oscillation Index (SOI_Dep)
Houston mean passage-period temperature (Hou_Pas_Temp)	Winter-period North Atlantic Oscillation (NAO_Win)
Houston mean passage-period wind speed (Hou_Pas_Wind)	Oklahoma City passage-period precipitation (OKC_Pas_Prec)
Fargo total passage-period precipitation (Far_Pas_Prec)	Omaha passage-period precipitation (Oma_Pas_Prec)
Wichita total passage-period precipitation (Wic_Pas_Prec)	Omaha mean passage-period wind speed (Oma_Pas_Wind)
Passage-period North Atlantic Oscillation (NAO_Pas)	Sioux Falls total passage precipitation (Sfa_Pas_Prec)
Mean winter North Atlantic Oscillation (NAO_Win)	Winnipeg, MB mean passage-period temperature (Win_Pas_Temp)
Departure-period Southern Oscillation Index (SOI_Dep)	Winnipeg, MB total passage-period precipitation (Win_Pas_Prec)
Year (Year)	Year (Year)
Previous year's arrival of breeding godwits in Beluga (Prev_Arrival)	Previous year's arrival of breeding godwit at Churchill (Prev_Arrival)

Akaike's information criterion (AIC; Burnham and Anderson 2001). I also analyzed both the entire Beluga data set (1974–2010) and that portion of the data set that corresponded to the exact years covered by the Churchill data set (1974–1994, 2008–2010) to ensure that any interpopulation differences were not driven by climate events in the period for which arrival data were unavailable for Churchill. I then standardized each variable in the best models and used them to identify the most important predictor variables from each model (Gelman 2008).

Finally, I took the best model(s) for each population and created a combined variable set that included the variables identified as important for each population, and then conducted the second stage of my analysis. To do this, I compared four models: a model in which only the predictor variables from a site were linked with the best model for that site (i.e., Churchill variables with a Churchill model) and three models in which the predictor variables from both sites were linked with the best model from one site (i.e., Churchill variables with a Beluga model). The comparison of these four models allowed me to detect whether godwits from the two populations responded to a set of climatic features unique to each population, or whether one set of climatic features was capable of predicting the migratory behavior of both populations.

RESULTS

Trends in Arrival Dates and Spring Temperatures

From 1974 to 2010, first arrival of godwits in south-central Alaska became earlier by 8.9 days (r^2 = 0.25, $P < 0.005$, $n = 37$), whereas in Churchill it became later by 10.6 days ($r^2 = 0.19$, $P < 0.05$, $n = 23$) (Figure 1.2). Spring temperatures also diverged between the two sites, although the trends were not significant: mean May temperatures rose in south-central Alaska (1.03°C, r^2 = 0.08, $P < 0.1$, $n = 37$) and cooled in Churchill (–1.39°C, $r^2 = 0.021$, $P < 0.40$, $n = 23$) (Figure

1.3). Coefficients of variation for May temperatures at the two sites, however, were dramatically different: 12.0% for Anchorage and 321.7% for Churchill (Bartlett's test, $P < 0.01$, $n = 2$).

Along godwit migration routes, relatively few weather variables showed systematic changes through the study period (Figure 1.4), but significant climatic changes occurred at godwit wintering sites. During the period that Alaskan godwits overwinter on Isla Chiloé, November through March, maximum temperatures rose (0.8°C, $r^2 = 0.14$, $P < 0.05$, $n = 37$) and total precipitation (–493.2 mm, $r^2 = 0.12$, $P < 0.05$, $n = 37$) and mean wind speed (–4.6 km h^{-1}, $r^2 = 0.70$, $P < 0.01$, $n = 37$) declined. Conversely, on Tierra del Fuego, where Churchill godwits overwinter from November through April, maximum temperatures dropped (–1.0°C, $r^2 = 0.17$, $P < 0.05$, $n = 37$) and minimum temperatures rose (0.8°C, $r^2 = 0.16$, $P < 0.05$, $n = 37$), and mean wind speed rose over the entire period (5.4 km h^{-1}, $r^2 = 0.22$, $P < 0.01$, $n = 37$) and during the month of April (5.76 km h^{-1}, $r^2 = 0.14$, $P < 0.05$, $n = 37$).

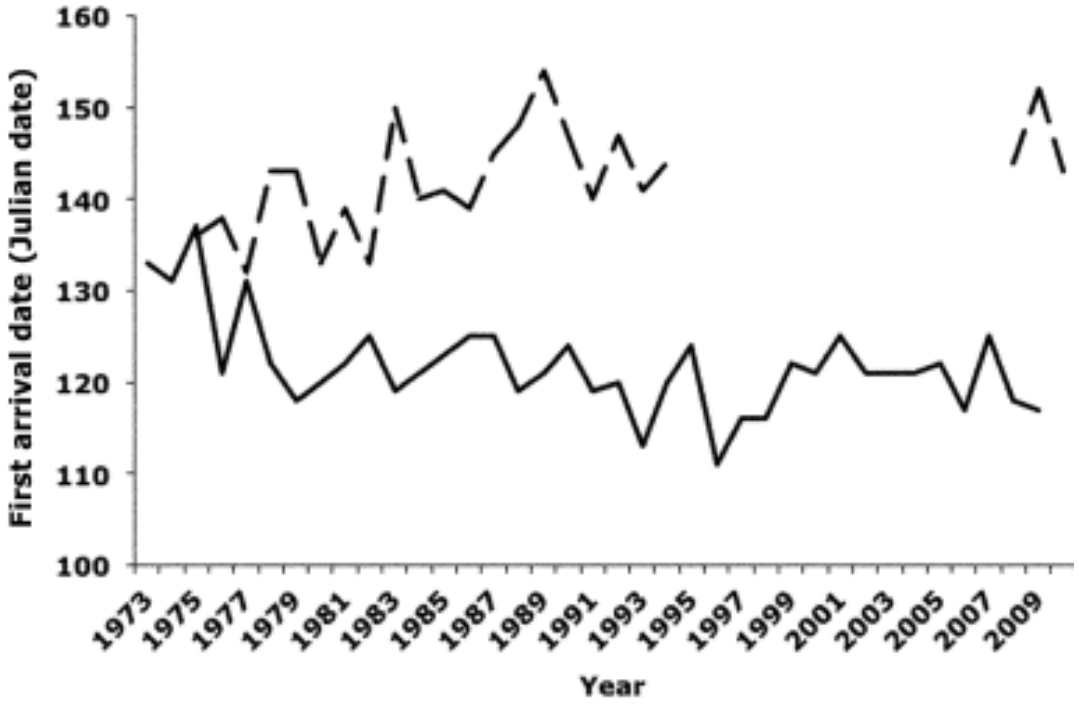

FIGURE 1.2: First-arrival dates of Hudsonian Godwits breeding in Churchill (dashed line) and Beluga River (solid line), 1973–2010.

Model Results

The first stage of my analyses showed that weather along the migration corridor (i.e., the bottleneck models) best accounted for variation in arrival dates (Table 1.2). The best model for Churchill included four terms, with an adjusted r^2 value of 0.74 and model weight of 0.37 (Table 1.3). The next-best model had a ΔAIC_c score of 0.6 and model weight of 0.28, and included the same four variables plus the addition of one variable and two interaction terms (Table 1.2). The best model for Beluga included five terms and one interaction term and had an adjusted r^2 value of 0.67 and model weight of 0.99 (Table 1.3). A reanalysis of the limited Beluga data set (removing the years for which Churchill arrival data were unavailable) yielded largely the same results: the bottleneck model with interactions remained at the top, with the addition of the prior-cue-use model as indistinguishable using ΔAIC_c scores ($\Delta AIC_c = 0.33$).

Not only did the models that best predicted arrival dates for the two populations differ as a whole, but the single most important predictors of godwit arrival dates also differed between the populations. Using standardized predictor variables, the variable identified as most important by the best Churchill model was the current year's mean May temperature at Churchill (estimate ± SE = −8.31 ± 10.63; Table 1.3). Three significant variables were identified in the best Beluga model: 5-year mean May temperature from Anchorage (−5.06 ± 1.58), March SOI (−9.69 ± 3.47), and an interaction term between the total winter precipitation from Puerto Montt and the March SOI (14.90 ± 4.03) (Table 1.3).

In the second stage of analysis, combining data from both populations, the best-supported model treated each population's arrival date as being predicted by different factors (Table 1.4). Models in which data from both populations were assigned to the variables in the top Churchill and Beluga models received little support ($\Delta AIC_c = 17.1$, 12.1, and 7.6, respectively).

TABLE 1.2: Model selection to estimate the factors affecting the timing of arrival on the breeding grounds of Hudsonian Godwits at Beluga River, Alaska, and Churchill, Manitoba, using linear regression models and AIC_c weights. (Only the top 10 of 22 models are shown for each analysis.) Parameters are defined in Table 1.1.

Model description	Parameters	df	Loglik	AIC_c	ΔAIC	w_i
		Beluga River				
Bottlenecks with interactions + large-scale climate	Anc_5yr+Anc_Prev_Arr+ Prev_Arrival+Hou_Pas_Wind+ SOI_Mar*PMC_Precip	9	–89.41	191.2	0.00	0.99
Bottlenecks without interactions + large-scale climate	Anc_5yr+Anc_Prev_Arr+Hou_ Pas_Wind+SOI_Mar+ PMC_Precip+PMC_Apr_Wind	8	–92.17	205.3	14.1	<0.01
Bottlenecks without large-scale climate	Anc_5yr+Prev_Arrival+ Anc_Prev_Arr+ Hou_Pas_Wind*PMC_Precip	8	–93.10	207.2	15.9	<0.01
Breeding grounds past temperatures	Anc_5yr+Anc_Prev_Arr	4	–99.14	207.5	16.3	<0.01
Breeding grounds temperatures	Anc_Apr_Temp+Anc_5yr+ Anc_Prev_Arr	5	–97.95	207.8	16.5	<0.01
Breeding grounds past weather	Prev_Arrival+Year+Anc_5yr+ Anc_Prev_May+ Anc_Prev_Snow+Anc_5yr_Sn	8	–93.55	208.1	16.8	<0.01
Breeding grounds + wintering grounds	PMC_Mean_temp+PMC_Precip +PMC_Dep_Wind+Prev_Arriva l+Anc_5yr+Anc_Prev_Arr+ Anc_Prev_Snow+Anc_5yr_Sn	10	–90.93	210.8	19.6	<0.01
Breeding grounds previous year	Prev_Arrival+Anc_Prev_May+ Anc_Prev_Tot	5	–103.08	218.0	26.8	<0.01
Breeding-grounds snow	Anc_Apr_Snow+Anc_Prev_Sno w+Anc_Tot_Snow+ Anc_Prev_Tot+Anc_5yr_Sn	7	–102.22	222.2	30.9	<0.01
Wintering grounds	PMC_Mean_temp+PMC_Precip +PMC_Dep_Wind	5	–106.49	224.9	33.6	<0.01

Model description	Parameters	df	Loglik	AIC_c	ΔAIC	w_i
	Churchill					
Bottlenecks without interactions	YYQ_Arr_Temp+ Oma_Pas_Wind+ RG_Rainy_Days+RG_Dep_Wind	6	–46.31	109.6	0.0	0.37
Bottlenecks with interactions + large-scale climate	YYQ_Arr_Temp+ NAO_OM*Oma_Pas_Wind+ RG_Dep_Wind*RG_Rainy_Days	9	–39.63	110.1	0.6	0.28
Bottlenecks without interactions + large-scale climate	YYQ_Arr_Temp+ Oma_Pas_Wind+NAO_OM+ RG_Rainy_Days+RG_Dep_Wind	7	–44.94	110.9	1.3	0.19
Bottlenecks with interactions	YYQ_Arr_Temp*Oma_Pas_Wind+RG_Rainy_Days*RG_Dep_Wind	6	–43.86	113.3	3.8	0.06
Current-year breeding grounds + wintering grounds	YYQ_Arr_Temp+ RG_Rainy_Days+RG_Dep_Wind+RG_Mean_Temp	7	–48.25	113.4	3.9	0.05
Bottlenecks with interactions + past breeding grounds	YYQ_Arr_Temp*YYQ_5yr+Oma_Pas_Wind+RG_Rainy_Days	6	–46.27	113.5	4.0	0.05
All current-year temperatures	YYQ_Arr_Temp+Hou_Pas_Temp+Win_Pas_Temp+RG_Mean_Temp	6	–51.00	118.9	9.4	<0.01
Bottlenecks with interactions + breeding grounds past + large-scale climate	YYQ_Arr_Temp*YYQ_5yr+NAO_OM*Oma_Pas_Wind+RG_Dep_Wind*RG_Rainy_days	11	–39.03	122.1	12.5	<0.01
Midcontinental winds	Oma_Pas_Wind+RG_Dep_Wind+Hou_Pas_Wind	5	–57.36	128.1	18.5	<0.01
Current-year breeding grounds	YYQ_Arr_Temp	3	–61.45	130.1	20.5	<0.01

TABLE 1.3: Parameter estimates for models with lowest AIC_c scores (from Table 1.1) for the Beluga River and Churchill populations of Hudsonian Godwits.

Parameter	β	SE	*t*
Beluga River			
Intercept	171.34	22.58	7.59
Previous arrival	–1.23	1.27	–0.97
Anchorage 5-year mean May temperature	–5.06	1.58	–3.21
Anchorage previous May temperature	–2.11	1.10	–1.93
Houston mean passage wind	2.22	1.04	2.14
Southern Oscillation Index March	–9.69	3.47	–2.79
Puerto Montt winter precipitation	–3.06	2.03	–1.51
Southern Oscillation Index March*Puerto Montt precipitation	14.90	4.03	3.70
Churchill			
Intercept	129.97	10.63	12.23
Churchill current-year mean May temperature	–8.31	1.53	–5.43
Omaha mean passage wind	3.41	1.68	2.03
Rio Grande winter rainy days	–1.53	1.90	–0.80
Rio Grande mean departure wind	–0.26	1.54	–0.17

DISCUSSION

The two populations investigated in the present study share most of the same migration corridor, breed at roughly the same latitude, and have bottleneck models as the best explanation of their arrival dates. Yet the two populations are strikingly different, both in recent trends in the timing of their arrival on their breeding grounds and in the factors that affect that timing. This dissimilarity stems from the confluence of different historical regional phenologies and recent warming trends.

Effects of Historical Phenology

Beluga River sits between a maritime climate to the south and east and a continental climate to the north and west. Spring occurs earlier in the region than elsewhere at the same latitude and with timing roughly similar to that in many areas much farther south (Figure 1.4A). For a godwit to arrive in south-central Alaska at the exact onset of spring, it must either make a long, nonstop flight directly to its breeding range from a location well to the south or stop and wait nearby at a site where spring has yet to begin. Historical reports of godwit concentrations and flyway temperatures support the nonstop-flight hypothesis; AKN records show that the northernmost April staging areas are in northern Kansas and southern Nebraska (Figure 1.1A), with only sporadic observations at sites farther north. Historical April temperatures also show that potential stopover sites farther north are usually still below freezing (Figure 1.4B).

TABLE 1.4: Parameters and model-selection criteria, based on Akaike's information criterion (AIC), for models for the combined, second-stage analysis. This second-stage analysis compares the most well supported models from the first-stage analysis to determine if the same climate and weather conditions affect the migration timing of both the Churchill, Manitoba and Beluga River, Alaska populations of Hudsonian Godwits.

Model Description	**Parameters**	**df**	**Loglik**	**AICc**	**ΔAIC**	w_i
Nested Model	Fiveyr:BU+Fiveyr:CH+ Prev_Arrival:BU+Prev_Arrival:CH+ Prev_May:BU+Prev_May:CH+ Bot_Wind:BU+Bot_Wind:CH+ Win_Prec*SOI_Mar:BU+ Win_Prec*SOI_Mar:CH+Cur_Yr:CH +Cur_Yr:BU+Win_Prec:BU+ Win_Prec:CH+Win_Wind:BU+ Win_Wind:CH	20	-124.76	314.22	0	0.976
Beluga Model	Fiveyr+BP+Prev_Arrival+Prev_May+ Bot_Wind+Win_Prec:SOI_Mar	8	-151.35	321.83	7.6	0.022
Churchill Model(1)	BP+Cur_Yr+Bot_Wind+Win_Prec+ Win_Wind	7	-155.02	326.32	12.1	0.002
Churchill Model(2)	BP+Cur_Yr+NAO_OM*Bot_Wind+Win_Prec+Win_Wind	9	-154.74	331.30	17.1	<0.001

[1] Paremeter Abbreviations: BU = Beluga River; CH = Churchill; Fiveyr = five-year mean May temperature from each population's breeding site; Prev_Arrival = the date of the previous year's arrival at each population's breeding site; Bot_Wind = the mean wind speed from the month of passage at each population's respective bottleneck; Win_Prec = the total precipitation from each population's wintering sit; SOI_Mar = the March Southern Oscillation Index value; Win_Wind = the mean wind speed during the non-breeding period for each population's wintering site; Cur_Yr = the mean May temperature from each population's breeding site; NAO_OM = the mean North Atlantic Oscillation value for October-March.

The necessity of a long-distance flight from Kansas or Nebraska to reach their breeding sites means that Alaska-breeding godwits are unable to stop anywhere close enough to their breeding grounds to encounter conditions that are closely correlated with those on the breeding grounds. This presumably explains why godwits breeding in south-central Alaska rely heavily on two cues derived from their previous years' experiences. For instance, April temperatures in Wichita, Kansas, are uncorrelated with those in Anchorage ($r = 0.04$). Among-year variation in Anchorage May temperatures, however, is relatively small, and both the 5-year average and mean May temperature exhibit roughly the same rate of change over the past four decades (slopes = 0.04°F and 0.02°F, respectively).

These results suggest that Alaskan godwits use cues from previous years to time their arrival. This strategy is successful because of the relatively slow rate of change and small variation in springtime temperatures in south-central Alaska. Although the use of intermediate stopover sites might be advantageous in some warm years (Drent et al. 2003), a long, nonstop flight is the safer migration strategy (Lank et al. 2003, Gill et al. 2009). Although rare, instances of conditions from previous years affecting the timing of future events are not unheard-of (Durant et al. 2004) and suggest both overriding constraints on the amount of time necessary to complete an annual cycle and the heightened plasticity of long-lived organisms (Morris et al. 2008).

Western Hudson Bay also intersects two climate regimes—boreal and Arctic. As such, the region vacillates between early, warm "boreal" springs and late, cold "Arctic" springs. Unlike in south-central Alaska, spring arrives later in Churchill than in other areas at the same latitude (Gagnon and Gough 2005b), and migrating godwits en route to Churchill pass through habitats where spring is already well advanced. This is borne out both by regional temperatures

along their migration corridor (Figure 1.4B) and by AKN records (Figure 1.1B). These circumstances enable Churchill godwits to stop far enough north to encounter conditions correlated with those on their breeding grounds (e.g., May temperatures in Winnipeg and Churchill are significantly correlated, $r = 0.42$), allowing them to use current-year conditions to time their arrival on the breeding grounds. Consistent with this hypothesis, I found that the best variable in each of the top three Churchill models was mean May temperature in Churchill itself.

Recent and Future Climate Change

The fact that different suites of environmental factors are correlated with two populations' migration timing suggests significant intraspecific flexibility in migration strategies, but also divergent trajectories for the two populations in the face of a changing climate. The climate-change regimes that affect the two breeding grounds are drastically different. Churchill has experienced long-term spring cooling, but substantial summer and winter warming, over the past decade (Gagnon and Gough 2005a, Kaufman et al. 2009). Conversely, south-central Alaska has seen slow, steady warming throughout the year (Soja et al. 2007). Projections for the near future suggest more of the same for both regions, with winter warming being especially pronounced, but a secondary summer warming peak also predicted for Hudson Bay (Gagnon and Gough 2005a).

What has kept the Churchill population from responding to these recent summer warming trends? Long-term trends in May temperatures along the Churchill population's migration route suggest that the constraint lies in contrasting climate-change regimes among different regions of interior continental North America. The three most southerly cities included in the Churchill model analysis have warmed in May over the past 37 years (mean slope = 0.033°F), whereas the

FIGURE 1.3: Hypothesized migration routes and model results for Hudsonian Godwit populations at Beluga River, Alaska, and Churchill, Manitoba. Solid lines and left-hand side of figure refer to Beluga River population; dashed lines and right-hand side of figure refer to Churchill population. Graphs (clockwise from upper left) show trends for each variable included in the best models for each population over the 37-year study period. (A) Five-year mean and previous year's mean May temperatures from Anchorage, Alaska; (B) current year's mean May temperature from Churchill; (C) mean May wind speed in Omaha, Nebraska; (D) mean April wind speed and total number of rainy days, November–April, in Rio Grande, Argentina; (E) total November–March precipitation in Puerto Montt, Chile, and March Southern Oscillation Index; and (F) mean April wind speed in Houston, Texas.

Temperature (Degrees Celsius)
Year
5-yr Mean May Temperature
Previous Year's Mean May Temperature
Mean Wind Speed (kmh)
Year
April Mean Wind Speed
Current Year's Mean May Temperature
May Mean Wind Speed
Mean Temperature (Degrees Celsius)
Year
Mean Wind Speed (kmh)
Year
November-April Rainy Days
April Mean Wind Speed
Number of Rainy Days
Mean Wind Speed (kmh)
Year
March SOI
October-March Precipitation
Total Precipitation (mm)
Southern Oscillation Index
Year

three most northerly cities all have cooled (mean slope = –0.039°F) (Figure 1.4B). This spring cooling contrasts with the long-term summer warming in Churchill (Gagnon and Gough 2005b) and means that the population is forced to reconcile conflicting trends (Strode 2003, Both 2010). With future climate scenarios projecting a continuation of these contrasting trends (Gagnon and Gough 2005a), Churchill godwits may soon face an untenable situation in which an earlier arrival is necessary because of a faster progression of breeding-season conditions, but simultaneously precluded by an ever later onset of spring (Strode 2003, Hüppop and Winkel 2006). Ongoing work has found that godwit breeding phenology at the site has been mismatched with local resource phenology by an average of 8 days and that this has led to extremely low breeding success, which suggests that the situation may already be untenable (N. R. Senner and B. K. Sandercock unpubl. data).

The Churchill population has few options that could remedy its current mismatch. One possibility would be for them to time their arrival on the basis of the previous summer's weather conditions (akin to the Alaska population). This would allow them to respond to changes in the phenology of resources critical to their breeding success but in some years would cause them to arrive during dangerously cold and inclement late-winter weather (Gagnon and Gough 2005a). Shorebird species that breed farther north frequently encounter such conditions, forcing them to rely on accumulated energy reserves until conditions ameliorate and feeding can resume (Morrison and Hobson 2004). Changing the timing cues used during migration may be difficult (Gwinner 1996, Helm et al. 2009), in spite of the fact that selection for properly timed breeding efforts is presumed to be significant (Visser and Both 2005). Alternatively, female godwits could reduce the amount of time between arrival and clutch initiation, but this is an unlikely solution given the limitations imposed by both physiology (Klaassen et al. 2001) and weather (Gagnon

and Gough 2005a).

Other studies have identified similarly conflicting trends affecting migratory species. In two of these studies (Ahola et al. 2004, Hüppop and Winkel 2006) the populations appeared not to have been negatively affected, because temperatures have warmed along their migration route but not on their breeding grounds, so that they now simply arrive earlier. Strode (2003) noted, however, that cooling spring temperatures have retarded northward-migrating parulid warblers in the north-central United States and likely cause phenological mismatches similar to those experienced by Churchill godwits. In that situation, only species that were able to rely on alternative early-spring prey were able to overcome the conflicting trends and maintain the proper breeding phenology (Strode 2003). This would be impossible for godwits arriving on snow-covered tundra.

By contrast, the Beluga population benefits from consistent warming trends across all seasons on the breeding grounds and along their entire North American migration corridor (for the five cities included in the Alaska models, mean slope = 0.027°F; Figure 1.4A; Soja et al. 2007). Consequently, the timing of Alaska godwits is not impeded and their breeding success remains robust (N. R. Senner and B. K. Sandercock unpubl. data). Current climate projections suggest that the warming trends will continue, in which case Beluga River godwits should be able to track regional climate change into the future (Soja et al. 2007, Wang et al. 2009).

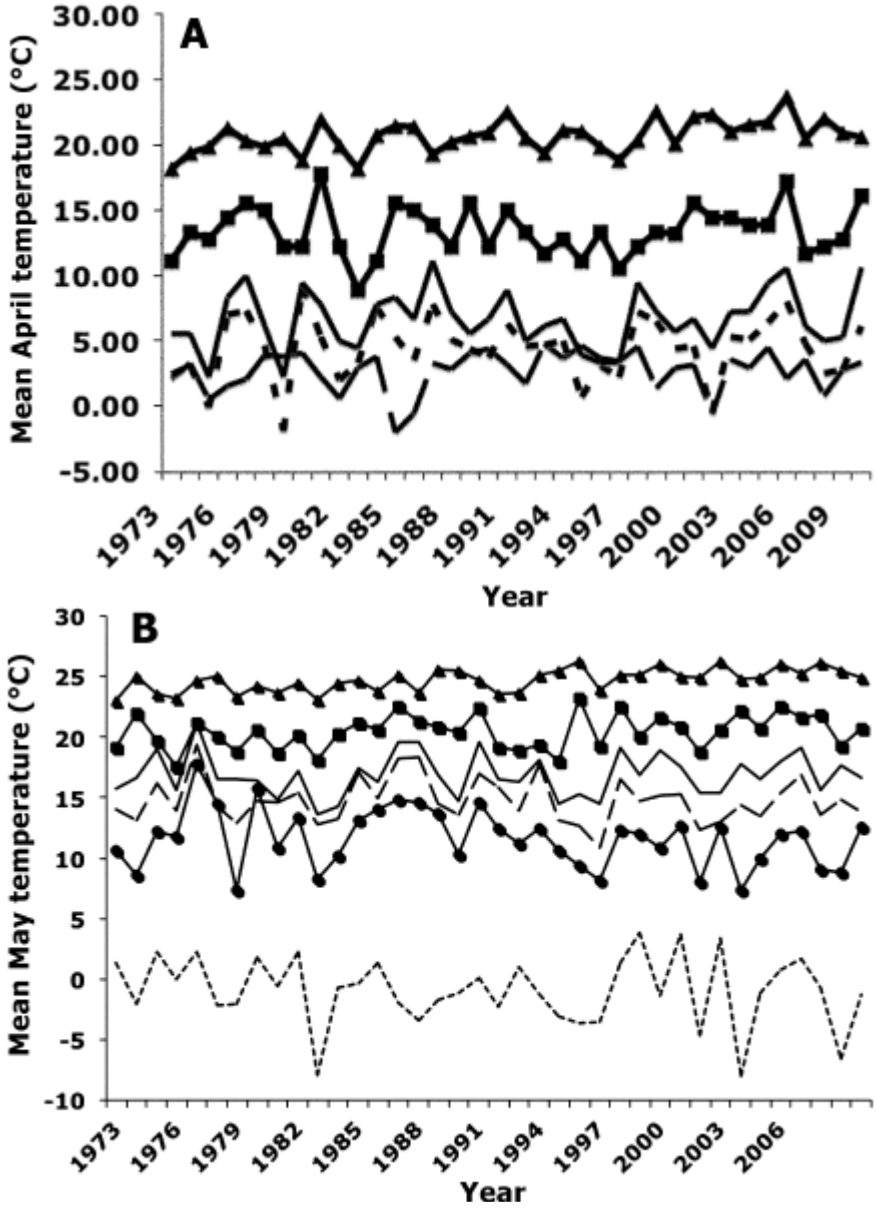

FIGURE 1.4: Mean (A) April and (B) May temperatures from the migration routes of the (A) Beluga River and (B) Churchill populations of Hudsonian Godwits, 1973–2010. In Figure 4a, cities are Anchorage (short-dash); Saskatoon (long-dash); Fargo (solid); Wichita (squares); and Houston (triangles). In Figure 4b, cities are Churchill (short-dash); Winnipeg (circles); Sioux Falls (long dash); Omaha (solid); Oklahoma City (squares); and Houston (triangles).

Bottlenecks

Bottleneck models were the best models for both Beluga and Churchill godwits. In spite of this similarity, significant differences exist between the conditions that affected the two populations. Only Beluga godwits were affected by a large-scale climate driver (SOI), whereas only Churchill godwits were affected by wind at their wintering site. These differences are significant, and even more striking is what these differences will mean for the future ability of the two populations to time their migrations successfully.

The most obvious difference between the two models is that March SOI was the only large-scale climate driver to be included in either of the top models. A host of other recent studies have found significant effects of large-scale climatic variables on the timing of passage and arrival on long-distance migrants (Hüppop and Hüppop 2003, Marra et al. 2005, Van Buskirk et al. 2009), but few have explored both large-scale climate drivers and local-scale weather variables in the same analysis. In the present analysis, SOI had the largest effect on Alaska godwits when combined with the effects of winter precipitation in Puerto Montt. This suggests that the true importance of large-scale climate drivers simply may be their influence on local-scale weather. The SOI matters only if it actually affects events at the scales at which godwits experience them. Although the SOI alters trade winds, storm tracks, and precipitation patterns throughout much of the Pacific Basin (Ropelewski and Halpert 1996, Harrison and Larkin 1998, Renault et al. 2009), it may be that the only weather feature both affected by the SOI and significantly affecting godwits is precipitation on their wintering grounds. Furthermore, SOI did not have a significant effect on Churchill godwit arrival, despite their presumed use of the Pacific Basin as a migratory corridor (Morrison 1984), further supporting its more localized effects. A study examining godwit migration only at the large scale would still pick up the

correlative influence of the SOI but would not pinpoint the appropriate scale and mechanism of its effect.

Current climate models project an increase in the frequency and strength of El Niño–Southern Oscillation (ENSO) events during the next century (Timmermann et al. 1999). Such changes to the climatic patterns of the Pacific Basin may, in the short term, have positive effects on the ability of Beluga godwits to arrive on their breeding grounds at progressively earlier dates. In the Beluga model, the interaction between March SOI and Puerto Montt precipitation was positively correlated with Beluga arrival dates and had the single largest effect of any variable (Table 1.1). As such, El Niño years are correlated with early arrivals of Beluga godwits on their breeding grounds, and their increased frequency may provide a boon to the population. At some point, however, either the frequency or severity of the droughts associated with ENSO events in southern South America could detrimentally affect the abundance of benthic invertebrates and the ability of godwits to prepare adequately for their northward migrations (Silva et al. 2006, Rubio-Álvarez and McPhee 2010).

Although weather conditions outside of the breeding season had less of an effect on Churchill godwits than did conditions on the breeding grounds, projected climate change in southern South America and midcontinental North America may further retard godwit arrival in Churchill. Climate change is currently progressing more slowly in southern South America than in other regions (Intergovernmental Panel on Climate Change 2007) but is projected to produce significantly less precipitation, higher temperatures, and the southward movement of storm tracks over the next century (Menéndez et al. 1999, Vera et al. 2006). Godwit arrival date was negatively correlated with precipitation and wind on Tierra del Fuego, which means that declines in precipitation and wind speed in the region may further slow godwit migration. Given the

negative relationship between midcontinental wind and Churchill godwit arrival date, the projected intensification of the low-level jet stream across midcontinental North America, especially in spring, will lead to higher winds in the region that may also impede Churchill godwits' migration (Cook et al. 2008). All told, climate-change projections for every variable included in the Churchill model suggest that Churchill godwits will have a difficult time altering their current trend in arrival date, even if spring conditions begin to warm in Churchill and along the northern portion of their migration route.

The dramatic differences between these two godwit populations, given their slightly different migration windows and migratory bottlenecks, speak to the importance of bottlenecks within the annual cycle (Warnock 2010). If recent climate change could already cause these divergences, the larger-scale changes projected to take place over the coming century may completely alter their migrations and breeding success. The conservation status of these two populations, especially in Churchill, likely will deteriorate.

Can Long-Distance Migrants Adapt to Climate Change?

Long-distance migrants make up a large proportion of the bird species that have been unable to respond successfully to phenological changes on their breeding grounds (Both et al. 2010, Moussus et al. 2011). Numerous hypotheses have been offered to explain these findings, mostly centered on the limitations of the cues used by long-distance migrants to initiate their northward migrations (Gwinner 1996, Both et al. 2005; but see Strode 2003). My study highlights that not all long-distance migrants are being adversely affected by phenological changes, and that population-level differences can exist within a single species even across similar latitudes. The success or failure of a population in tracking phenological changes is heavily influenced both by the specific climate-change regimes encountered along its migration route and by the reliability

of the available information about those regimes. Some populations may be tracking some phenological changes, but it may be impossible for a population to track them all (Strode 2003, Jonzén et al. 2007, Both 2010).

In the case of godwits, it is counterintuitive that the population with apparently less information about conditions on its breeding grounds is the one whose cues are better predictors of future breeding conditions there. However, the quantity of information available may be unrelated to the quality of that information (Fischer et al. 2011). Thus, although Churchill godwits can stop closer to their breeding grounds and potentially acquire more information about the conditions awaiting them farther north, this information is currently a poor predictor of the conditions they will experience during the breeding season.

This important distinction means that we may not be able to predict *a priori* which long-distance migrants, even those within a single habitat, will suffer a phenological mismatch as a result of climate change. With the availability of reliable cues, some long-distance migrants may have a better chance than previously thought to adjust successfully to climate change. Understanding the specific circumstances affecting each population is necessary for predicting its vulnerability to climate change.

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CHAPTER 2

ECOLOGICAL MISMATCHES IN A LONG-DISTANCE MIGRATORY BIRD: A TEST OF THE PHENOLOGICAL AND LIFE-HISTORY HYPOTHESES

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ABSTRACT

Ecological mismatches between avian reproductive events and the timing of seasonal peaks in food resource abundance are contributing to ongoing declines in migratory birds, particularly as the environmental impacts of climate change have accelerated during recent decades. The *life-history* hypothesis predicts that life-history traits, such as long-distance migration or diet specialization, are the best predictors of the vulnerability of an organism to ecological mismatches. Conversely, the *phenological* hypothesis argues that the climate change regimes experienced by populations at different stages of the annual cycle are a better predictor of ecological mismatches. To test the relative importance of life-history and phenological traits as potential causes of ecological mismatches, we documented the breeding phenology and reproductive success of two disjunct populations of Hudsonian Godwits, *Limosa haemastica*, breeding at Churchill, Manitoba and Beluga River, Alaska. The Churchill godwit population has experienced both warming and cooling climatic regimes at different stages of its annual cycle, resulting in an 8-day mismatch between the timing of hatch and the onset of peak invertebrate abundance during 2009-2011. In contrast, the Beluga River population has experienced only warming climatic regimes during its annual cycle, is not mismatched, and changes in its breeding

phenology have kept pace with recent climatic change. Ecological mismatches have affected godwit fitness: the Churchill population experienced low reproductive success, whereas the Beluga population had consistently higher reproductive success. We conclude that ecological regimes experienced by migratory animals during the annual cycle are an important risk factor leading to ecological mismatches. Assessments of conservation status are often based on life-history traits but the key role of phenological traits must be considered when identifying the populations most likely to experience ecological mismatches induced by climate change.

INTRODUCTION

Global climate change has caused a broad range of phenological changes in different environments and trophic levels, including the earlier bud burst of perennial plants (Bennie *et al.* 2010), earlier arrival of migratory birds at breeding sites (van Buskirk et al. 2009), and earlier emergence of mammals from hibernation (Adamik and Kral 2008). One of the most commonly identified effects of phenological change has been a decoupling of the timing of breeding by migratory species and the peak abundance of local food resources used by those species to feed dependent young (Dunn and Winkler 2010). The mismatch-hypothesis posits that migratory species fail to adapt to phenological changes at their breeding sites because the environmental cues used to time their migratory movements are not changing at the same pace (Durant et al. 2007). Failure to adapt has meant that migratory species are unable to time the rearing of young with peaks in local resource phenology and thus suffer lower reproductive success in a resource-poor environment (Both and Visser 2005). The mismatch hypothesis has been invoked to explain widespread declines of long-distance migratory birds in recent decades (Møller et al. 2008; Jones and Cresswell 2010). Evidence for ecological mismatches is relatively rare, however, and a

growing number of field studies have failed to find mismatches (Dunn et al. 2011). As global climate change accelerates, conservation efforts would be aided by a better understanding of the underlying mechanisms that create ecological mismatches.

The *life-history* hypothesis posits that six life-history traits predispose species to ecological mismatches: long-distance migration, use of continental migratory routes, use of seasonal habitats with temporally limited resource peaks, diet specialization, slow rates of reproduction, and high annual survival (Thomas et al. 2006; Amano and Yamaura 2007; Møller et al. 2008; Both et al. 2010; Davis et al. 2010). For example, the Dutch breeding population of the Pied Flycatcher, *Ficedula hypoleuca*, exhibits many of these traits—it migrates 5000 km to the Sahel zone of sub-Saharan Africa, breeds in temperate deciduous forests where it relies on the seasonal emergence of winter moths, *Operophtera brumata*, to provision young, is breeding out of synchrony with peak caterpillar abundance, and is suffering severe population declines (Both and Visser 2001; Both et al. 2005). However, other bird populations that also meet most of the six criteria show no evidence of ecological mismatches (Both et al. 2006; Tulp and Schekkerman 2008; Dunn et al. 2011). Red Knots, *Calidris canutus canutus*, winter in West Africa and breed in western Siberia, have annual survival greater than 80%, and rely on the brief peak in Arctic insect abundance to raise their young (Buhler and Piersma 2008; Leyrer et al. 2012). Nevertheless, this population has not developed a mismatch as a result of recent climate change (Schekkerman et al. 2003; Tulp and Schekkerman 2008). Conversely, ecological mismatches have been reported in some bird species that do not have any of the six life-history traits identified as risk factors, including the resident, short-lived, Great Tit, *Parus major* (Visser et al. 1998; Goodenough et al. 2010).

The *phenological* hypothesis argues that phenological traits associated with the timing of

life-history events may be better predictors of ecological mismatches than life-history traits (Lyon et al. 2008). Phenological traits include variation in the direction and rate of climatic change at breeding sites, conflicting patterns of climate change encountered at different sites during the annual cycle, and annual variation in the predictability of environmental conditions (Strode 2003; Hüppop and Winkel 2006; Both 2010; Visser et al. 2010). Phenological traits may work singly or in concert, but could affect populations by determining the reliability of environmental cues that individuals use to time life-history events during their annual cycles (Thomas et al. 2010). In Pied Flycatchers, the populations experiencing the most severe ecological mismatches have conflicting climate change regimes amongst their non-breeding sites, migration routes, and breeding sites (Both 2010). Conversely, timing of breeding in Arctic populations of Common Eider, *Somateria mollissima*, has remained in synchrony with local resource phenology because the cues predicting resource availability have remained reliable, despite dramatic changes in regional climate conditions (Love et al. 2010). These lines of evidence provide support for the phenological hypothesis, but more empirical tests are needed.

Hudsonian Godwits, *Limosa haemastica*, (hereafter, 'godwits') are long-distance migrants that traverse the entire length of the Western Hemisphere during their annual cycle. Godwits nest in highly seasonal Arctic and sub-arctic wetland habitats, lay only a single clutch of four eggs per year, do not reach sexual maturity until three years of age, and can live up to 30 years or longer (Walker et al. 2011). Phenological changes throughout the species' annual cycle have been dramatic, as Arctic and sub-arctic ecoregions are warming faster than the rest of the globe (IPCC 2007). In previous work, we showed that two disjunct godwit populations are facing differing climate change regimes at different sites during the course of their annual cycles and have had differential responses to these changes (Chapter 1). Godwits breeding at Churchill,

Manitoba have retarded their arrival at their breeding sites because of cooling spring temperatures that have preceded long-term, rapid early summer warming. In contrast, godwits breeding at Beluga River, Alaska have accelerated their arrival dates over the same period in response to synchronous patterns of spring and summer warming. Intraspecific differences between Hudsonian Godwits at two breeding sites provide an opportunity to test for the potential causes and mechanisms leading to ecological mismatches in two independent populations with a shared evolutionary history.

We tested the phenological hypothesis by *i*) examining differences between the climatic and phenological regimes experienced by our two study populations and *ii*) testing how environmental differences affect the synchrony between the timing of breeding events and local resource abundance. The life-history hypothesis predicts that both populations should be mismatched, as godwits at both breeding sites share the same six life-history traits. However, the phenological hypothesis predicts that the godwits breeding at Churchill, but not the Beluga River population, should be mismatched with local food resources because only that population has experienced conflicting phenological regimes during its life-cycle.

METHODS

Study Species

Hudsonian Godwits breed in three disjunct populations — southcentral and western Alaska, the Arctic of northeastern Alaska and the Northwest Territories, and the western Hudson Bay lowlands of Manitoba and Nunavut. We studied godwits in two of the three populations — southcentral Alaska and northern Manitoba. Breeding birds in these two regions are known to have separate non-breeding ranges: Godwits from coastal Alaska winter along the Pacific coast

of southern Chile, whereas godwits from Hudson Bay winter along the Atlantic coast of continental Argentina and the island of Tierra del Fuego (Walker et al. 2011, Chapter 1).

Migratory timing and breeding phenology differ substantially between the two populations. Godwits breeding in southcentral Alaska depart from non-breeding sites in Chile during the first week of April, arrive at breeding sites in southcentral Alaska during the last week of April, and begin egg-laying during the first few days of May. In contrast, birds breeding in the Hudson Bay lowlands leave their non-breeding sites in Argentina a month later during the first week of May, arrive at breeding sites in northern Manitoba during the last week of May, and begin egg-laying by the end of the first week of June (Walker et al. 2011, Chapter 3). Reproductive effort is similar in both populations: females usually lay a single clutch of four eggs (although, if the first is depredated, a replacement clutch may be laid), both parents jointly incubate the eggs for 22-23 days, and both parents attend the young for 14-20 days after hatching. Timing of hatch differs between our study populations by one month, with an average hatch date of 1 June at Beluga River, Alaska and 1 July at Hudson Bay, Manitoba (Walker et al. 2011).

The two populations have been exposed to different climate change regimes. Southcentral Alaska has experienced steady year-round warming that has led to an increase of 3°C in mean annual temperatures since 1950 (Serreze et al. 2001). Patterns of climate change in western Hudson Bay are more complicated: a slow warming trend in summer (Jun-Aug) and winter (Nov-Mar) persisted through the late 1990s (Hinzman et al. 2005), but has been followed by a dramatic increase in warming during these periods in the 2000s (Kaufmann et al. 2009). Over the past few decades, however, western Hudson Bay has also experienced cooling during some months, especially May, and even more rapid warming during others, such as early June

and mid March (Gagnon and Gough 2005b).

The climate change regimes experienced by the two populations differ not only at their breeding sites, but also at stopover sites used during migration. Beluga River godwits migrate northward during the month of April, and have experienced consistent warming regimes along their entire migration path, which follows a continental route through central North America. Churchill godwits migrate along a similar route a month later in May, but are met with a different pattern of climate regimes, because long-term trends for climatic change have included late spring cooling in the northern Great Plains of the United States and Canada (Chapter 1).

The combination of historical differences in the timing of migratory movements, combined with differential patterns of climate change, has caused the two populations to diverge dramatically in their migratory phenologies over the past four decades. Compared to arrival dates of godwits recorded in the early 1970s, Alaskan godwits now arrive at their breeding sites nearly 9 days earlier, whereas Hudson Bay godwits arrive nearly 11 days later (Chapter 1).

Field Methods

From 2009-2011, we monitored the breeding success of godwits at two study sites corresponding to the geographic centers of the southcentral Alaska and Hudson Bay breeding populations: Beluga River, Alaska (61.21°N, 151.03°W) and Churchill, Manitoba (58.93°N, 93.80°W). Study sites ranged in size from 8 km^2 at Beluga River to 15 km^2 at Churchill, and both sites supported large breeding populations of godwits (densities: 5.0 breeding pairs per km^2 at Beluga, and 2.3 pairs per km^2 at Churchill; N.R. Senner unpubl. data). Both study sites are dominated by sedges, *Carex* spp., and dwarf birch, *Betula nana*, although they appear superficially different — the Churchill study site is located on a large, open fen, while the Beluga River site is situated in a black spruce, *Picea mariana*, dominated muskeg bog (Walker et al. 2011; N.R. Senner, unpubl.

data)

We surveyed breeding godwits from adult arrival in spring (mean = 1 May ± 5 d and 22 May ± 5 d at Beluga and Churchill respectively; Chapter 1) until southward departure at the completion of the breeding season (mean = 2 July ± 8 d and 17 August ± 16 d respectively; Senner et al. in review). We started nest searching after pair formation was completed and found nests using behavioural cues from the attending parents and by opportunistically flushing incubating individuals. We monitored nests every 2-3 days until a nest had either hatched or failed (depredated or abandoned). On most visits, we checked nests by resighting incubating birds with binoculars at distances of 20-30 m and flushed incubating birds once each week to minimize disturbance that might increase the probability of nest failure. At hatch, we captured nestlings by hand at the nest and uniquely marked each with an alpha-numeric flag and a uniquely numbered metal band on the tibiotarsus (USGS or Canadian Wildlife Service). To examine brood movements and chick survival, we randomly selected one chick per brood to receive a 0.62 g Holohil (model BD-2) or 0.65 g ATS radio (A1015) for telemetry monitoring. We clipped the downy feathers from a small area of the backs of chicks and attached radios immediately above their uropygial gland with Loctite 454 cyanoacrylate glue (Pearce-Higgins and Yalden 2004).

We triangulated locations of radio-marked chicks every 2-3 days until chicks had either died or survived until the completion of the brood-rearing period. To monitor chick growth, but minimize handling time, we recaptured chicks once per week throughout the brood-rearing period (Sharpe et al. 2009). If a chick went undetected on a visit, we attempted to relocate the chick by radio-telemetry for three consecutive days. A chick undetected after three days was considered dead. We considered a chick to have successfully survived the brood-rearing period if

it survived to an age of 21 days. Godwits usually fledge at 28 days (Walker et al. 2011), but 21 days was the average lifespan of our radios (range = 17-30 days) and the age by which most adults abandon their broods (Walker et al. 2011).

Environmental Variables

We tested three environmental variables as correlates of intra- and inter-annual variation in daily survival and growth of godwit chicks: temperature, precipitation, and wind speed. These three variables can have direct or indirect effects on shorebird young by affecting time-budgets for activity or the availability of invertebrate prey (Both and Visser 2001; Smith et al. 2007; Schekkerman et al. 2009). Daily weather records were taken from nearby weather stations at Anchorage, Alaska (50 km from the Beluga River field site) and the village of Churchill, Manitoba (26 km from the Churchill field site) and accessed through NOAA's Climate Data Online webpage, http://www.ncdc.noaa.gov/cdo-web/search. Climatic conditions during the chick period were measured from the 40 d periods of 1 June-10 July at Beluga River and 30 June-8 August for Churchill.

The abundance and availability of invertebrate prey are two of the most important factors potentially affecting the early survival of precocial shorebird young. Without an adequate food supply, chicks may be unable to grow at the rapid rate required during the short northern growing seasons (Schekkerman et al. 2003), may not be able to thermoregulate during inclement weather (Beintema and Visser 1989), or may be less able to escape from predators (Cresswell and Whitfield 2008; Schekkerman et al. 2009). We used two measures of food availability in our candidate models for chick survivorship — a 32 d window centred on the timing of peak invertebrate biomass (average biomass per day; 32 d corresponds to the period of time chicks are present on the study site) and daily invertebrate biomass.

We measured insect biomass along two 100 m transects deployed on representative godwit territories that were randomly selected during the first year of the project and maintained thereafter (Schekkerman et al. 2003). Each transect consisted of five pitfall traps, which were cleared each morning at 07:30. Each pitfall trap was 10 cm wide, 15 cm deep, and filled with 4 cm of 75% ethanol to ensure that invertebrates were both trapped and preserved. Samples were identified to (sub)Order and body length was measured to the nearest 0.5 mm. Dry mass of invertebrates was calculated using published estimates of taxa-specific length-mass relationships (Rogers et al. 1977; Ganihar 1997). Shorebird young are potentially gape-limited and we therefore restricted our analyses to invertebrates of intermediate size classes (2-9 mm) that could potentially be consumed by chicks (Schekkerman and Boele 2009).

Statistical Analyses

To develop a mechanistic understanding of godwit reproductive performance, we examined how environmental covariates affected chick growth and then tested for a relationship between chick growth and survival. We created separate growth curves for godwit young captured at each site in each year, using the "nlme" function and a logistic growth equation in the "nlme" library in program R (ver. 2.10.1, R Development Core Team 2009). The logistic growth function calculates age-specific mass (M_t) by:

$M_t = A/(1 + \exp(-K(t - i)))$

where A = asymptotic body size of adults, K is the logistic growth coefficient, t = age in days, and i = the inflection point for maximal growth ($0.5A$ in the logistic function). We captured few chicks during the later stages of the brood-rearing period, and opted to set asymptotic mass (A) to be the mean body mass for adult godwits at each site (Austin et al. 2011; N.R. Senner unpubl. data). Using site and year-specific growth curves, we determined a body-condition index for

each individual at each recapture by dividing the observed growth rate since last capture by the expected growth rate using the logistic equation (Schekkerman et al. 2003). We then used a linear mixed-effects model with individual as a random effect to model different environmental factors that determine chick growth (function "lmer" in library "lme4" in program R; ver. 2.10.1, R Development Core Team 2009).

We used known fate models to estimate nest and chick survival. Individual encounter histories for each nest and radio-marked chick were developed and analysed with the "nest survival" procedure of Program Mark (Version 5.1, White and Burnham 1999). The nest survival procedure is a known fate model suitable for analyses of nest monitoring or "ragged" telemetry data (Mong and Sandercock 2007). Encounter histories required four input variables for each nest or chick: k = date of first encounter (e.g., date of nest discovery or attachment of radio transmitter to chick), l = date last known to be alive (e.g., last encounter), and m = date of completion (e.g., date nest hatched or failed; date young fledged or died); finally, each individual chick or nest was assigned one of three possible fates (f)—known alive, known dead, or uncertain (for when a radio-marked chick disappeared and no radio or dead chick was found). Using these four inputs, we calculated daily survival rates (s) of radio-marked chicks separately for each year and site and daily survival as a function of environmental and individual covariates. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection to identify the best model(s) among our set of candidate models (Burnham and Anderson 2001). Timing and duration of breeding differed between our two study sites and we opted to test for site differences in survival with a posthoc test in Program Contrast (Sauer and Williams 1989).

Last, we tested whether ecological mismatches affected current or historical breeding

success of godwits at each site. To identify current mismatches, we used a factorial ANOVA with the fixed effects of period and year to compare the mean daily biomass of invertebrates during the 32 d brood-rearing period versus a 32 d period centred on the annual peak in invertebrate abundance. To identify historical mismatches, we used generalized linear models (the "glm" function in program R) to identify the climatic variables that best predicted observed daily invertebrate abundance. We then used the resulting regression equations and historical daily weather conditions to "hindcast" predicted daily invertebrate abundance at both sites during the past four decades (Tulp and Schekkerman 2008).

RESULTS

Nest Survival

Seasonal patterns in nest survival at both sites were best explained by a quadratic function where nest survival was highest at the start and end of the nesting seasons. At Churchill, the minimum AIC_c model contained an interaction between year and a quadratic function for day of season (Year × Quad) and had $w_i = 0.998$, with all other candidate models receiving little support (w_i <0.01; Table 2.1). At Beluga River, the minimum AIC_c model was also a model with an interaction between year and a quadratic function (Year × Quad; $w_i = 0.30$), although two other models received similar levels of support — a model with a linear function for day of the season (Lin, $\Delta AIC_c = 0.1$, $w_i = 0.28$) and a model with an interaction between year and a linear function for day of the season (Year × Lin, $\Delta AIC_c = 1.4$, $w_i = 0.15$) (Table 2.1).

The probability of nest survival differed strongly between sites and among years (Figure 2.1, Table 2.2). Godwits at Churchill had lower nest survival (exposure period = 23 d) than birds at Beluga River in each of

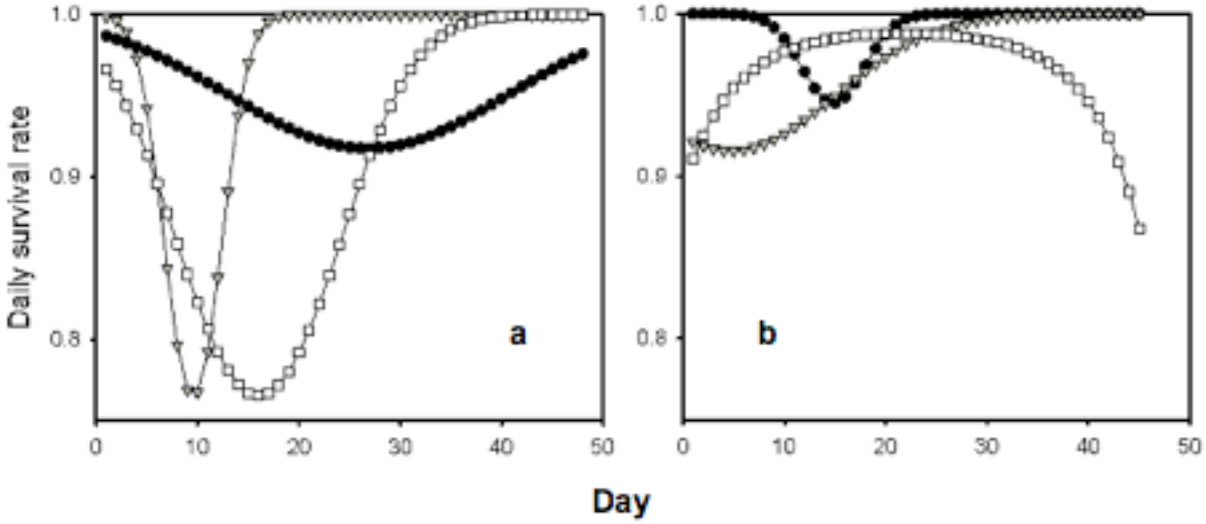

FIGURE 2.1: Seasonal variation in daily survival for nests of Hudsonian godwits breeding at (a) Churchill, Manitoba and (b) Beluga River, Alaska 2009-2011. Estimates of daily nest survival were taken from model S (year × quad) where seasonal trends were modeled as a quadratic function of day of season in each year. In 5 of 6 comparisons, daily survival rates were lowest during the middle of the nesting period. Black circles denote 2009, gray triangles denote 2010, and white squares denote 2011. Day 1 = 5 June at Churchill and 5 May at Beluga River.

TABLE 2.1: Model selection for the effects of temporal covariates on daily survival rates of Hudsonian godwit nests at Beluga River, Alaska and Churchill, Manitoba, 2009-2011.

Model	K	Deviance	AIC_c	ΔAIC_c	w_i
Beluga River					
Year × Quad	9	151.4	169.6	0	0.30
Lin	2	165.7	169.8	0.1	0.28
Year × Lin	6	158.9	171.0	1.4	0.15
Quad	3	165.2	171.2	1.6	0.14
Year + Lin	4	164.5	172.6	3.0	0.07
Null	1	171.8	173.8	4.1	0.04
Year + Quad	5	164.2	174.2	4.6	0.03
Year	3	170.8	176.8	7.2	0.01
Daily	45	137.2	231.4	61.8	0.00
Year + Daily	47	135.6	234.2	64.5	0.00
Churchill					
Year × Quad	9	148.8	167.2	0	1.00
Year × Lin	6	169.1	181.3	14.1	0.00
Year + Lin	4	175.5	183.6	16.3	0.00
Year + Quad	5	174.1	184.2	17.0	0.00
Lin	2	182.6	186.7	19.4	0.00
Quad	3	181.2	187.3	20.0	0.00
Year	3	189.4	188.5	21.2	0.00
Null	1	139.5	191.4	24.2	0.00
Year + Daily	50	144.5	251.9	84.7	0.00
Daily	48	107.0	251.9	84.7	0.00

[1] Year = a model treating each year separately; Quad = a model applying a quadratic trend with day of season; Lin = a model applying a linear trend with day of season; Daily = a time-dependent model with a different daily survival rate for each day of the season; Null = an intercept-only model, + = additive or main effects model, and × = factorial model with main effects and an interaction term.

TABLE 2.2: Probability of survival for nests and chicks of Hudsonian Godwits breeding at Churchill, Manitoba and Beluga River, Alaska, 2009-2011. Probability of survival was calculated from daily survival rates for 23 d and 21 d exposure periods for nests and chicks, respectively. Variance of extrapolated estimates was calculated with the delta method.

Site	Year	Estimate	SE	n
		Probability of nest survival (23 d)		
Churchill	2009	0.17	0.14	15
	2010	0.32	0.29	26
	2011	0.04	0.02	16
	Pooled	**0.17**	**0.15**	**57**
Beluga River	2009	0.71	0.27	23
	2010	0.56	0.29	22
	2011	0.65	0.27	25
	Pooled	**0.64**	**0.29**	**70**
		Probability of chick survival (21 d)		
Churchill	2009	0.06	0.03	6
	2010	0.23	0.13	16
	2011	0.04	0.01	11
	Pooled	**0.13**	**0.07**	**33**
Beluga River	2009	0.18	0.11	17
	2010	0.03	0.01	18
	2011	0.27	0.16	24
	Pooled	**0.15**	**0.09**	**59**

the three years, with the lowest survival rates observed in 2011. Beluga River had less interannual variation, but survival was lowest in 2010.

Chick Growth

Chick growth rate tended to be higher at Churchill than Beluga River, but did not significantly differ between sites (ANOVA, $F_{1,4} = 0.11$, $P = 0.75$). At Churchill, asymptotic mass was fixed at $A = 239$ g, growth rate was estimated to be $K = 0.13 \pm 6.84 \times 10^{-7}$, and the inflection point, $i = 16.4 \pm 2.27 \times 10^{-5}$ d. At Beluga River, asymptotic mass was fixed at $A = 249$ g, and $K = 0.12 \pm 2.5 \times 10^{-3}$ and $i = 18.9 \pm 0.25$ d. Growth rates differed among years at both sites ($\Delta AIC_c = 6.99$ for models with and without year as a fixed effect; Figure 2.2). For Churchill, growth rate was lowest in 2009 ($K = 0.12 \pm 0.01$) and highest in 2010 ($K = 0.14 \pm 0.01$), while, for Beluga River, growth rate was highest in 2010 ($K = 0.13 \pm 0.01$) and lowest in 2011 ($K = 0.12 \pm 0.01$).

Growth rates of godwit young were affected by different environmental conditions at each site. The minimum AIC_c model at Beluga River contained hatching date, insect abundance, wind, minimum temperature, and precipitation as fixed effects and individual as a random effect ($w_i = 0.26$). Slope coefficients were largest for hatching date and minimum temperature and a majority differed significantly from zero (Table 2.3). The next best-fit model ($\Delta AIC_c = 0.43$, $w_i = 0.21$) included all of the same variables except for insect abundance. For Churchill, the minimum AIC_c model contained individual as a random effect and hatching date, minimum temperature, and precipitation as fixed effects ($w_i = 0.54$). Hatching date was the best predictor of chick growth and was the only individually significant predictor (Table 2.3). The next best model included the mean and maximum daily temperatures as covariates ($\Delta AIC_c = 1.59$, $w_i = 0.24$).

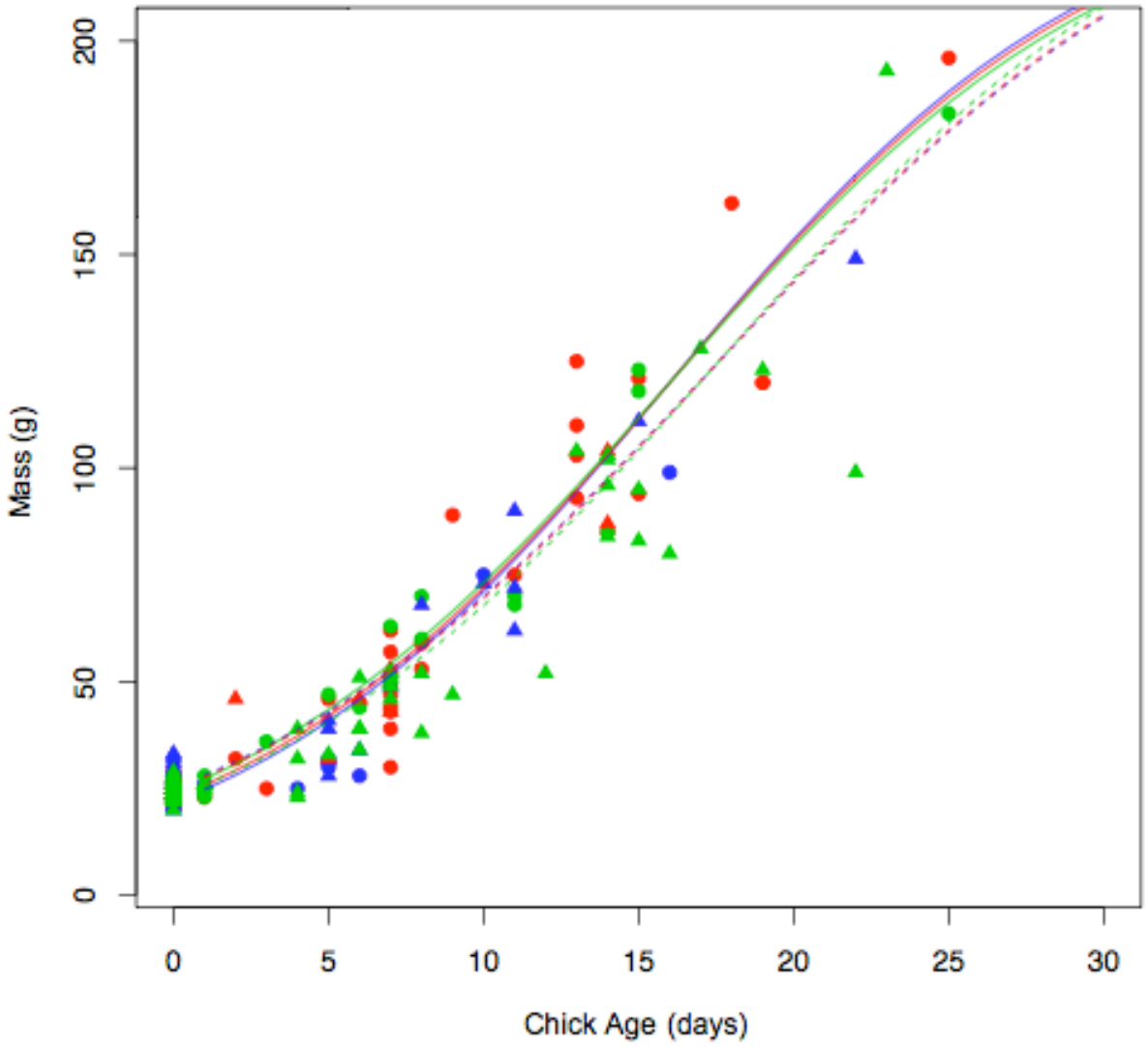

FIGURE 2.2: Annual growth curves for Hudsonian Godwit chicks hatched at Churchill, Manitoba and Beluga River, Alaska during 2009-2011. Circles and solid lines are for Churchill chicks, triangles and dashed lines for Beluga River chicks (2009 is blue, 2010 is red, and 2011 is green). Growth curves were fitted using the logistic growth function where asymptotic mass (*A*) was fixed at a site-specific mass (Churchill = 239 g, Beluga River = 249 g) and year was included as a random variable. We monitored growth and survival of radio-marked chicks until 21 days and fledging occurred at day 28.

TABLE 2.3: Model coefficients for factors explaining growth rates of Hudsonian Godwit chicks at Beluga River, Alaska and Churchill, Manitoba, 2009-2011. All environmental conditions are measured on a daily time scale.

Parameters	Random Effects			Fixed Effects				
	Variable	Variance	SE	Variable	Estimate	SE	*t*-value	*P* ≤
				Beluga River				
Hatching Date + Mean Wind Speed + Minimum Temperature + Precipitation	Ind.	38.04	0.86	Intercept	239.59	69.77	3.43	0.01
				Hatching Date	-1.55	0.46	-3.41	0.01
				Mean Wind Speed	-9.21	3.30	-2.79	0.01
	Residual	95.67	1.37	Minimum Temperature	6.64	2.12	3.14	0.01
				Precipitation	2.55	2.05	1.24	0.15
				Churchill				
Hatching date + Minimum Temperature+ Precipitation	Ind.	0.00	0.00	Intercept	33.81	28.18	1.20	0.15
				Hatching Date	-0.12	0.06	-1.79	0.05
	Residual	3.46	0.35	Minimum Temperature	0.17	0.20	0.85	0.20
				Precipitation	-0.02	0.02	-1.00	0.20

Chick Survival

The two sites differed from one another in the key environmental conditions that best predicted chick survivorship (Table 2.4). At Beluga River, an additive model containing year, linear effect of day of season, and chick age was the minimum AIC_c model (Year + Lin + Age; $w_i = 0.69$), while the second best model was an additive model containing day of the season and chick age as covariates (Lin + Age; $\Delta AIC_c = 2.2$, $w_i = 0.23$). At Churchill, there was no single best model of chick survival and eight models had $\Delta AIC_c < 2.0$ (Table 2.4), including models with insect abundance (Insect; $\Delta AIC_c = 0.5$, $w_i = 0.11$) and mean daily temperature (Year + Temperature; $\Delta AIC_c = 1.2$, $w_i = 0.07$).

Survival of radio-marked godwit chicks to 21 days differed among years at each site (Figure 2.3, Table 2.2). At Beluga River, chick survival was high in two of three years, but was 7-11 times lower in 2010 (Table 2.2). At Churchill, the opposite was true: survival was low in two of the three years, but was 4-6 times higher in 2010 (Table 2.2). Chick survival did not differ significantly between sites (post-hoc test, $\chi^2 = 0.03$, df = 1, $P = 0.86$), but Beluga River tended to have higher survival rates than Churchill (0.152 ± 0.145 vs. 0.128 ± 0.145, $n = 3$ years).

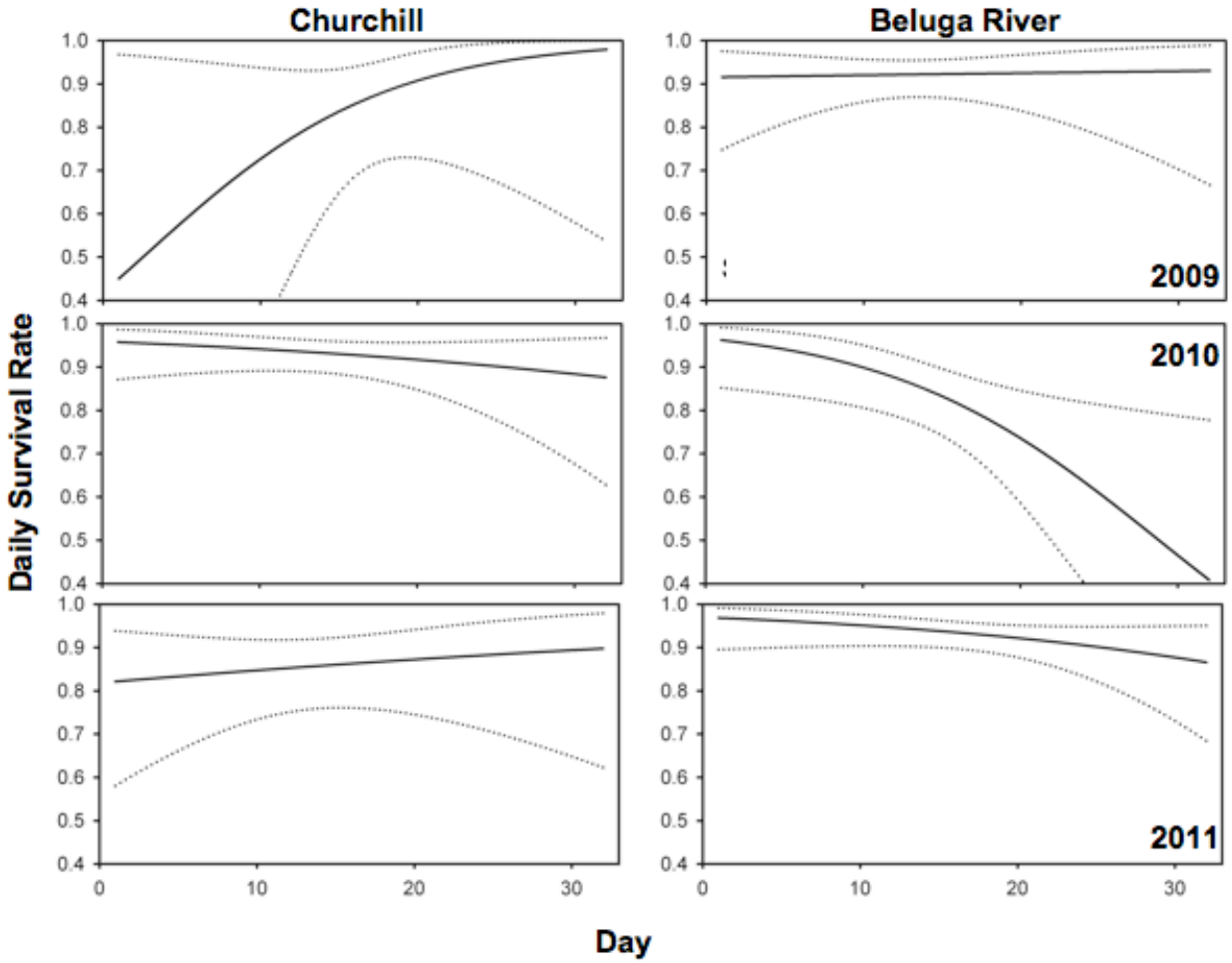

FIGURE 2.3: Seasonal variation in daily survival rates (±95%CI) of Hudsonian Godwit chicks hatched at (a) Churchill, Manitoba and (b) Beluga River, Alaska, 2009-2011. Daily survival rates were taken from a model S (year × lin) where seasonal trends were modeled as a linear function of day of season in each year. Day 1 for Churchill was 1 July and for Beluga River was 31 May.

TABLE 2.4: Model selection for the effects of covariates on daily survival of Hudsonian Godwit chicks hatched at Beluga River, Alaska and Churchill, Manitoba, 2009-2011.

Model	K	Deviance	AIC_c	ΔAIC_c	w_i
Beluga River					
Year + Lin + Age	5	205.1	215.2	0	0.69
Lin + Age	3	211.4	217.4	2.2	0.23
Year + Lin	4	213.3	221.4	6.2	0.03
Year × Lin	6	209.9	222.0	6.8	0.02
Year + Insect	4	216.5	224.6	9.4	0.01
Year	3	218.9	225.0	9.8	0.01
Year × Temperature	6	213.6	225.7	10.5	0.00
Year + Temperature	4	217.8	225.9	10.6	0.00
Year × Insect	6	214.3	226.5	11.3	0.00
Year + Age	4	218.4	226.5	11.3	0.00
Churchill					
Year	3	126.6	132.6	0	0.13
Insect	2	129.0	133.1	0.5	0.11
Year × Insect	6	121.0	133.4	0.8	0.09
Year + Temperature	4	125.6	133.8	1.2	0.07
Year × Temperature	6	121.5	133.8	1.2	0.07
Year + Age	4	125.7	133.8	1.2	0.07
Temperature	2	129.8	133.8	1.2	0.07
Lin	2	130.5	134.6	2.0	0.05
Year + Insect	4	126.5	134.7	2.1	0.05
Year + Lin+ Age	5	124.5	134.7	2.1	0.05

[1] Year = a model that treats year as a covariate; Lin = a model applying a linear trend with day of season; Age = a model that includes chick age as a covariate; Temperature = a model that includes mean daily temperature at the breeding site as a covariate; and Insect = a model that includes mean daily insect abundance as a covariate. × denotes a factorial model, while + an additive model.

Current Mismatches in Seasonal Phenology

Godwit nests at Churchill hatched on average 8 ± 5 d (n = 3 years) after the onset of the 32 d peak phenological window of invertebrate biomass. In contrast, godwits at Beluga hatched on average 8 ± 1 d (n = 3 years) before the onset of the peak phenological window. Daily invertebrate abundance was lower during the brood-rearing period than the phenological peak of emergence in both populations (Figure 2.4). Differences in insect biomass between the peak period and chick period were marginally significant at Churchill (ANOVA, $F_{1,186} = 3.45$, $P = 0.06$), but were not significant at Beluga River ($F_{1,186} = 0.55$, $P = 0.46$). Insect abundance varied significantly among years at both Churchill ($F_{2,186} = 7.33$, $P < 0.01$) and Beluga River ($F_{2,186} = 7.24$, $P < 0.01$), but interactions between period and year were nonsignificant ($F_{2,186} < 0.63$, $P > 0.53$). Variability in daily insect abundance was also higher during the chick period than it was during the phenological peak for both populations. In Churchill, the mean coefficient of variation for invertebrate abundance was significantly higher during the chick period (77.4 ± 0.02%) versus during the phenological peak as well (70.7 ± 0.03%; Bartlett's test, df = 1, $P = 0.04$). Within years, variability was significantly higher only during 2010 (Bartlett's test, df = 1, $P = 0.02$). At Beluga, the mean coefficient of variation during the chick period was 71.3 ± 0.1%, while during the phenological peak it was 63.7 ± 0.11% (Bartlett's test, df = 1, $P = 0.42$). Variability in vertebrate abundance was not significantly different within years at Beluga.

TABLE 2.5: Model coefficients for factors explaining the effects of daily weather conditions on daily invertebrate abundance at Beluga River, Alaska and Churchill, Manitoba, 2009-2011. All environmental factors were measured on a daily timescale.

Variable	β	SE	$P \leq$
	Beluga River		
Intercept	-1.97×10^{4}	3.90×10^{3}	0.01
Mean Sea Level Pressure	19.45	3.85	0.01
Mean Wind Speed	-3.12	0.62	0.01
Maximum Temperature	337.4	63.43	0.01
Precipitation	-291.6	119.3	0.01
Julian Date^2	2.57×10^{-3}	7.15×10^{-4}	0.01
Dewpoint^2	-0.03	9.13×10^{-3}	0.01
Mean Sea Level Pressure * Maximum Temperature	-0.33	0.06	0.01
Mean Wind Speed * Precipitation	20.17	9.52	0.01
	Churchill		
Intercept	9.28×10^{5}	4.08×10^{-5}	0.01
Maximum Sea Level Pressure	-6.20×10^{4}	2.72×10^{4}	0.01
Mean Dewpoint^2	254.1	143.6	0.05
Mean Humidity^2	-182.1	43.56	0.01
Max Sea Level Pressure^2	1.04×10^{3}	453.8	0.01
Degree Days^2	-5.76×10^{-5}	8.07×10^{-6}	0.01
Julian Date^2	7.14×10^{-3}	1.66×10^{-3}	0.01
Maximum Wind Speed	-2.93	1.07	0.01
Maximum Sea Level Pressure * Mean Dewpoint^2	-16.93	9.58	0.06
Maximum Sea Level Pressure * Mean Humidity^2	12.15	2.91	0.01
Degree Days^2 * Maximum Wind Speed	8.23×10^{-7}	2.40×10^{-7}	0.01
Mean Dewpoint^2 * Maximum Sea Level Pressure^2	0.28	0.16	0.05
Mean Humidity^2 * Maximum Sea Level Pressure^2	-0.20	0.05	0.01

Historical Mismatches in Seasonal Phenology

Regression equations for hindcasting historic daily insect abundance data were created using NCDC weather data collected from 2009-2011. For Beluga, using a backward stepwise regression process, the best model had an adjusted R^2 value of 0.26 (df = 194, $P < 0.01$) and included six variables and two interaction terms (Table 2.5). The best Churchill model had better performance with an adjusted R^2 value of 0.52 (df = 98, $P < 0.01$) and had seven variables and five interaction terms (Table 2.5).

Using the site-specific regression equations (Table 2.5), hindcasting indicated that the date of peak insect abundance has shifted earlier over the past four decades at Beluga River but changed little at Churchill. At Beluga River, seasonal peaks in invertebrate abundance are estimated to occur 14 d earlier in 2010 than in the early 1970's (df = 36, $R^2 = 0.11$, $P = 0.05$), whereas at Churchill seasonal peaks occur at about the same time or slightly earlier (df = 35, $R^2 = 0.001$, $P = 0.83$). Interannual variation in the timing of the peak of invertebrate abundance, however, has increased significantly at both Churchill and Beluga River. In Churchill, the coefficient of variation for predicted invertebrate emergence (CV) during the initial 15-year period of the study, from 1974-1988, was 28.9%. Using a 15-year moving average, the CV peaked during the period from 1992-2006 (41.6%), before falling again during the most recent period from 1997-2011 to 33.1%, although no difference was statistically significant (Bartlett's test, df = 1, $P = 0.31$). At Beluga River, the CV during the 15-year period from 1974-1988 was 11.3% and peaked during the period from 1992-2006 (32.0%), a significant change from the initial 15-year period (Bartlett's test, df = 1, $P < 0.01$), and fell to 26.2% during the most recent period, 1997-2011 (Bartlett's test, df = 1, $P = 0.01$).

DISCUSSION

Differences in timing of breeding and demographic performance between Hudsonian Godwits breeding in southcentral Alaska and northern Manitoba supported the phenological hypothesis. Phenological traits associated with ecological conditions experienced during migration and early breeding were good predictors of whether the timing of breeding in godwit populations was mismatched with seasonal peaks in food availability. Godwits breeding in northern Manitoba encounter asynchronously changing climatic regimes at different stages of the annual cycle, resulting in an ecological mismatch and poor chick survival. In contrast, godwits in Alaska have experienced synchronously changing climatic regimes, remained in synchrony with their local resource phenology, and have maintained a relatively high level of reproductive success. Past assessments of population vulnerability to climate change have focused on the relative importance of variation in life-history traits (Thomas et al. 2006, Hutchings et al. 2012). Our results suggest that life history is insufficient to identify which populations are most in danger of experiencing ecological mismatches and what selective pressures may allow some populations to successfully respond or adapt to climatic change.

Ecological Mismatches in the Arctic

Godwits breeding at Churchill were mismatched with seasonal peaks in local abundance of invertebrates, with the onset of hatch occurring up to two weeks after the beginning of the window of peak abundance. The difference between invertebrate abundance in the peak window and the brood-rearing period was only marginally significant, but the brood-rearing period for godwit chicks always coincided with periods of lower invertebrate abundance and greater day-to-day variability in food availability. Thus, daily survival of chicks at Churchill was positively related to daily insect abundance. Insect abundance and temperature both had positive effects on

chick growth and survival, suggesting that starvation was an important cause of chick mortality.

At Beluga River, hatch of godwit nests began about one week prior to the onset of the peak phenological window in invertebrate abundance, such that the period of maximum chick growth coincided with peak invertebrate abundance. Chick growth but not survival was affected by invertebrate abundance at Beluga River, suggesting that most chicks died as the result of predation or other extrinsic factors acting on individuals in poor condition. Godwits at Beluga River experienced one year of extremely low reproductive success, but breeding failure did not result from a mismatch. In 2010, hatch began appropriately early, but chick survival was low because of inclement weather during the breeding season and unusually high predation rates (N.R. Senner unpubl. data).

Neither population showed seasonal declines in chick survival as predicted by the mismatch hypothesis (Dunn et al. 2011). Declines in invertebrate abundance after the phenological peak were nonlinear, but day-to-day variability in invertebrate abundance increased along with the probability that a given day would have low invertebrate abundance. For instance, across all years in Churchill, low densities of invertebrates (<50 mg per trap) occurred during only 27% of days during the peak period but over 39% of days during the chick period. Thus, it is possible for chicks that hatch after the peak to experience a period of relatively high insect abundance and survive to an age at which starvation is less likely (e.g., Churchill in 2010). On average, however, chicks hatched after the peak will encounter low resource abundance.

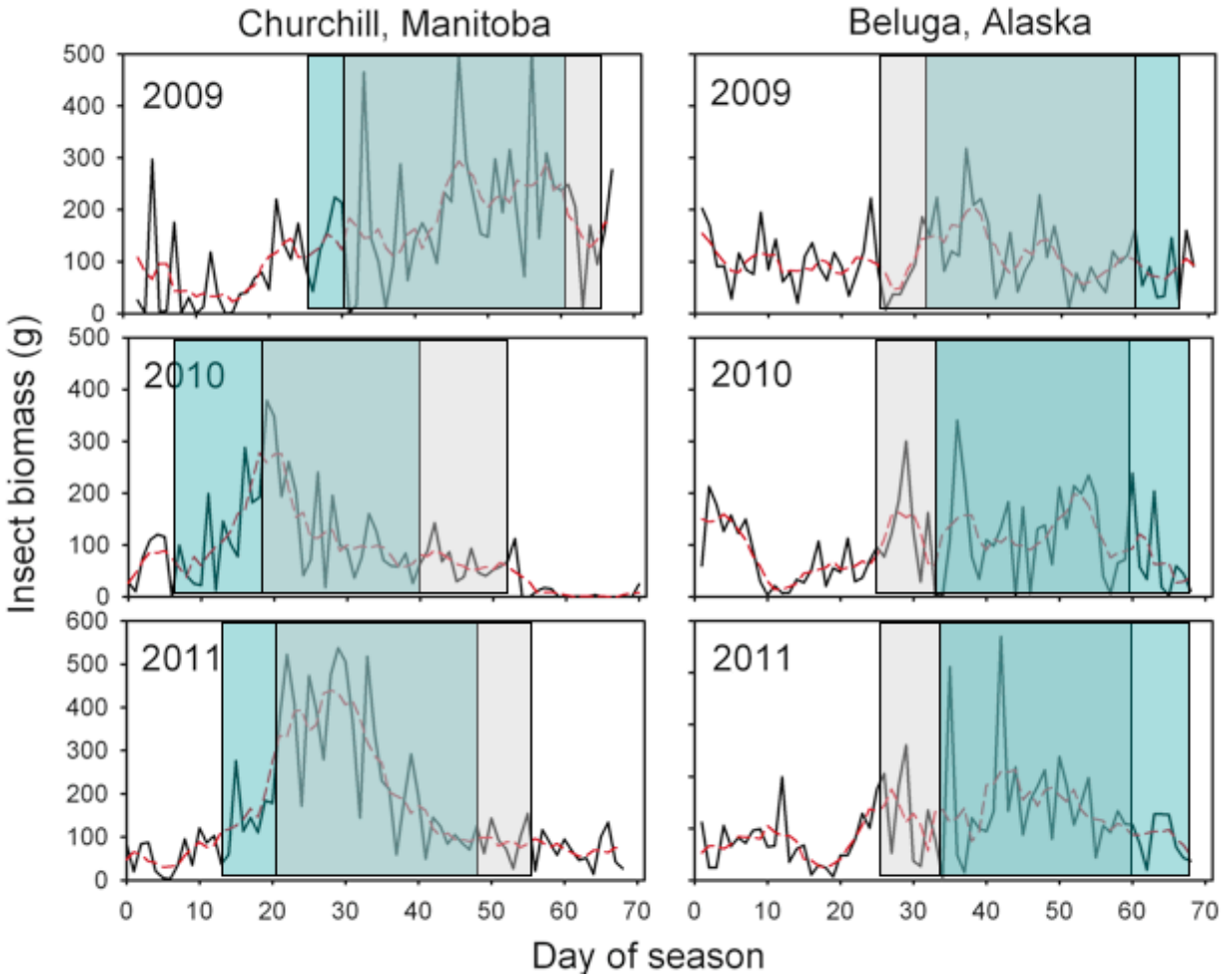

FIGURE 2.4: Chronological relationships between Hudsonian Godwit hatch dates and seasonal peaks in daily insect abundance at (a) Churchill, Manitoba (b) Beluga River, Alaska 2009-2011. The black line indicates daily measurements of insect biomass, the red line a smoothing function that subtracts a standard error value for each day. Gray boxes indicate the period of brood-rearing when godwits were attending young each year, beginning with the hatch of the first nest and ending with the fledging of the last chicks (32 days). Blue boxes indicate the 32 d period centered on peak mean daily insect abundance each season. The x-axis denotes day of the season (Day 1 for Beluga was 3 May, Day 1 for Churchill was 7 June).

Ecological mismatches between the timing of godwit breeding and environmental conditions at Churchill resulted from conditions in the sub-arctic environment and features of godwit breeding ecology. Scolopacid shorebirds are precocial and nidifugous. In such species, coping with inclement conditions or environmental variability via increased foraging rates is less feasible than in Arctic songbirds that have having biparental care (Beintema and Visser 1989, Schekkerman et al. 2003, Hoset et al. 2004, Tjørve et al. 2009). The environment at Churchill is an intrinsically highly variable low-arctic ecosystem that requires an elevated growth rate fuelled by higher feeding rates to allow chicks to fledge within a short summer season (Schekkerman et al. 2003, Gagnon and Gough 2005b, Williams et al. 2007). In high latitude ecosystems, reductions in resource quality or quantity are likely to have significant effects on chick survival. When coupled with a low rate of nest survival, ecological mismatches during the brood-rearing period may be resulting in regular breeding failure of this local population.

Causes of Ecological Mismatches

Our study shows that climate change regimes experienced by populations are the underlying cause of ecological mismatches in godwits. The Churchill population faces two climate-change hurdles that currently keep them from properly timing their breeding efforts. One factor is that asynchronous and contrasting climate change regimes are occurring along their migration route and during late spring and early summer on their breeding grounds. A second challenge is that variability in the timing of peak invertebrate abundance has also risen dramatically in Churchill, increasing by nearly 30% over the past four decades.

The combination of these two phenological changes suggests that godwits would need to change two aspects of their annual cycle to mitigate the impacts of their current ecological mismatch. First, godwits would have to adopt different proximate cues for timing their migratory

movements, switching from mean May temperatures at their breeding grounds to early summer temperatures at their breeding grounds from the previous year (Chapter 1). Second, even if selection were strong enough for Churchill godwits to alter their timing of arrival, they would also need to have significant additional plasticity in the timing of their migration to allow for such high environmental variability at these interior-continental breeding sites. A population may have some ability to respond to interannual variability in environmental conditions — by either speeding up or skipping certain portions of their annual cycle — but such adjustments may not be adequate to allow godwits to alter their arrival date by weeks at a time between consecutive years, especially given their reliance on environmental cues encountered at continental staging sites during spring migration (Chapter 1, Chapter 3). Overall, the current combination of phenological changes makes it unlikely that Churchill godwits will be able to overcome an increasing ecological mismatch quickly enough to cope with the rapid pace of future climate change (Gagnon and Gough 2005a).

Phenological Traits vs. Life-history Traits

Our field study joins a growing body of work reporting that long-term changes in phenological regimes determine a population's vulnerability to ecological mismatches (Åhola et al. 2004, Hüppop and Winkel 2006, Both 2010, Jones and Cresswell 2010). Ours is one of the first to consider both the phenological regimes encountered during migratory movements and the trophic mechanisms affecting breeding success (Chapter 1). Our results also provide new insights into why a particular suite of life-history traits alone does not necessarily result in a mismatch. Instead, we found that the phenological traits of a population are better predictors of whether a given population will be mismatched (Hüppop and Winkel 2006, Both 2010).

Gathering detailed information on phenological traits may be unrealistic for many

populations, especially species that cannot be tracked throughout their annual cycle or in which different populations mix during periods of the year. A diagnostic test to help identify and predict mismatches could be a valuable tool for conservation, but previous tests may have underestimated the number of species and populations suffering mismatches (Møller et al. 2008, Jones and Cresswell 2010). Jones and Cresswell (2010) proposed a two-part metric based on asynchronies between non-breeding and breeding sites to assess risk for 193 migratory bird populations. If sufficient data were available, greater predictive power might be realized with a four-part metric that combines the rate of climatic change during the 1) pre-migratory and 2) migratory periods and the rate of climatic change of the 3) arrival and 4) breeding periods at breeding sites (Hüppop and Winkel 2006, Chapter 1). Comparing these four periods independently would allow for the evaluation of the potential for asynchronously changing — and ecological mismatch inducing — climatic regimes throughout a population's annual cycle. A four-part metric would also partition stages of the annual cycle into the seasonal periods when migrants experience the greatest selection to alter the timing of breeding (Visser and Both 2005, Pulido 2007, Lyon et al. 2008).

Churchill godwits provide a clear example of conflicting trends at different points of the annual cycle (Table 2.6), but not all such examples necessarily lead to a mismatch (Ahola et al. 2004, Hüppop and Winkel 2006). The direction and timing of changes within the annual cycle may also play a role. In the case of Finnish Pied Flycatchers, spring temperatures are warming and summer temperatures are changing relatively little, leaving them a potentially longer window in which to prepare for the breeding season (Hüppop and Winkel 2006). Furthermore, for migrants crossing the equator during their migration, asynchrony between climate regimes at non-breeding sites and along their

TABLE 2.6: Comparison of long-term changes in temperature at different stages of migration for two breeding populations of Hudsonian Godwits at Beluga River, Alaska and Churchill, Manitoba, 1974-2010 (from Chapter 1).

	Temperature Trends			
Population	**Pre-Migratory Period (°C year^{-1})**	**Southern Portion of Migration Route (°C year^{-1})**	**Northern Portion of Migration Route (°C year^{-1})**	**Breeding Season (°C year^{-1})**
Beluga River	+0.002	+0.04	+0.02	+0.03
Churchill	+0.04	+0.03	-0.04	+0.03

migration route may be less important than ones occurring closer to their breeding sites, as such an asynchrony may leave more time for individuals to compensate for a delay prior to their arrival at their breeding grounds (Alerstam 2006, Both 2010).

Emphasizing the phenological traits of a population instead of the life-history traits affects our view of how selection and plasticity may shape the ability of populations to adapt to global climate change (Lyon et al. 2008). An emphasis on life-history traits focuses on selection for optimal timing in egg-laying and hatching in response to changes in environmental conditions during the breeding period (Both et al. 2009). Food resources are critical to the breeding success of a population and are the root causes of ecological mismatches. However, food resources or other environmental factors at breeding sites are unlikely to be the only proximate cues that migratory animals use to time events during their annual cycle (Lyon et al. 2008, Helm et al. 2009, but see Klaassen et al. 2001). Expanding our understanding of the phenological regimes at other stages of the annual cycle will allow for a more nuanced exploration of mismatches and their causes. The question changes from proximate mechanisms — Why is a population not arriving earlier (e.g., Jonzen et al. 2007)? — to ultimate explanations — What causes a population to arrive when they do (e.g., Hüppop and Winkel 2006)? — and facilitates identification of the key ecological factors driving mismatches in timing. Gaining a more complete understanding of ecological mismatches does not necessarily alter our predictions for how affected populations will fare as climate change accelerates, but we will find surprising insights into how migrants organize their annual cycles and what ability they do have to adapt and change.

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CHAPTER 3

BUFFER EVENTS EXPLAIN ABSENCE OF CARRY-OVER EFFECTS IN A MIGRATORY BIRD

Nathan Senner, Wesley Hochachka, James Fox, and Vsevelod Asfayanev

ABSTRACT

1. Migratory species face severe time constraints and physiological stresses, influences of which can carry over across seasons. It is unclear, however, under what conditions these carry-over effects arise and whether or how they persist within and across years.
2. Understanding when carry-over effects are created and how they persist is critical to identifying those points that constrain the annual cycle of a population and determining how selection is acting upon individuals throughout the entire year.
3. Using three consecutive years of full-cycle migration tracks and four consecutive years of breeding success data, we tested whether delays experienced during one migratory segment of the annual cycle of a long-distance migratory bird, the Hudsonian Godwit, *Limosa haemastica*, represent fitness costs that persist or accumulate across a godwit's annual cycle.
4. We found that some individual godwits repeatedly began to accumulate delays during specific parts of their annual cycle, but that certain events buffered them from these delays by absorbing previously accumulated delay. As a result, individuals did not suffer reductions in their breeding success.
5. The existence of these "buffer events" is important for understanding the selection

pressures experienced by migratory species but also emphasizes that high-quality stopover and wintering sites are critical to the maintenance of migratory populations.

INTRODUCTION

Migratory species, and especially those breeding at Arctic and sub-arctic latitudes, face severe time constraints during their annual cycles (Bêty et al. 2004). Many species must properly time their annual activities to correspond with resource peaks at disparate sites spread widely across the globe (Buehler and Piersma 2008). Migrants frequently incur significant stress during the course of their migratory movements and breeding efforts and this stress can alter the trade-off between current and future resource allocation (Harrison et al. 2011). There is an increasing recognition that these trade-offs do not just have short-term consequences, but also can carry over into future seasons and influence events that were previously believed to be disconnected (Norris 2005). Ultimately these carry-over effects can even affect population dynamics (Norris and Taylor 2006).

Carry-over effects have been documented in an array of species, not only long-lived migratory birds and ungulates, but also shorter-lived, largely sedentary organisms like reptiles, fish, and invertebrates (Harrison et al. 2011). Most studies have investigated how events occurring during the non-breeding season can alter the future breeding success of individuals. For instance American redstarts, *Setophaga ruticilla*, occupying lower-quality habitats during winter departed for and arrived on their breeding grounds later and had reduced breeding success (Marra et al. 1998, Norris et al. 2004). Similar findings in Icelandic black-tailed godwits, *Limosa limosa islandica*, and sockeye salmon, *Oncorhynchus nerka*, suggest that such effects are common across migratory taxa (Gunnarsson et al. 2005, Crossin et al. 2008).

Despite these efforts, and largely as a result of the continued difficulty in tracking individual migrants, there has been little effort to identify how carry-over effects are manifested during the non-breeding season or whether they persist or even accumulate over sequential life-history phases (Bogdanova et al. 2011). This leads to the question: When during the annual cycle do carry-over effects arise and when do they disappear? It is possible that once carry-over effects have been incurred, they never disappear; conversely there may be mechanisms in their annual cycle that reduce or even erase residual stress, limiting the persistence of carry-over effects. Identifying which of these alternatives is correct is key to understanding the selection pressures acting upon individuals throughout their annual cycles, but also critical for prioritizing conservation actions (Webster et al. 2002, Sheehy et al. 2010).

Here we present data taken from British Antarctic Survey geolocation-tracking devices placed on 26 adult Hudsonian Godwits (hereafter, godwits), *Limosa haemastica*, on their breeding grounds for three consecutive years coupled with four consecutive years of data on breeding success rates. Godwits migrate the entire length of the Western Hemisphere and must breed within the short, nine-week sub-arctic summer, meaning that their annual cycle is likely severely time constrained and increasing the likelihood that carry-over effects will have detrimental consequences (Conklin and Battley 2011). Therefore, we predict that those godwits falling behind during one portion of their annual cycle will either not recoup this lost time or subsequently fall further behind, resulting in a late arrival on the breeding grounds, a failure to nest during the narrow phenological peak for breeding, and reduced breeding success (Bêty et al. 2004).

METHODS

We studied breeding Hudsonian Godwits at Beluga River, Alaska (61.21°N, 151.03°W) from 2009-2012. Nests were discovered using behavioral cues or by opportunistically flushing incubating individuals. We determined the number of nesting attempts made by an individual by monitoring each nest every 2-3 days until the nest had either failed or hatched. Renests were found and monitored in the same manner as first nests. Upon hatch, all chicks in a brood were captured before leaving the nest and outfitted with U.S. Geological Survey metal bands and unique alpha-alpha flags. Godwits fledge at the age of 28 days (Walker et al. 2011) and once the earliest chicks to hatch had potentially reached that age, we surveyed our study site daily for fledged chicks. We denoted an individual adult as having bred successfully if one chick from its brood reached an age of at least 28 days. (In 2012, nests were followed until hatch, but chicks were not tracked to fledging.)

Individual adult godwits were captured on nests and outfitted with a U.S. Geological Survey metal band, a UV-resistant color band, and either a uniquely coded alpha-alpha flag or a British Antarctic Survey (BAS) Mk-14 or Mk-10 geolocation-tracking device (hereafter, logger) attached to a uniquely coded alpha-alpha flag (Figs. 3.1, 3.2). Mk-10 loggers weigh 1.4 g (2009) and Mk-14 loggers weigh 1.1 g (2010), roughly 0.44-0.56% of mean godwit lean mass (Walker et al. 2011). Flag-bearing loggers were attached to the left upper tibia and separated from the tibio-tarsal joint by the color band to reduce potential wear on the joint (Figure 3.1). Returning individuals with loggers were recaptured on their nests and given new loggers to monitor the subsequent year's movements.

After retrieval, movement data were downloaded and initially analyzed using BAS software (version 8, March 2010). BAS loggers measure ambient light levels once per minute and record the highest level from each five-minute period from throughout the deployment of the

logger. Light level information were transformed to identify the timing of sunrise and sunset for each day of deployment, which was, in turn, used to calculate the approximate location of the logger each day. There are limitations to the precision and accuracy of locations given by this method. As such, decision rules must be applied to the raw movement data so that errors caused by unusual shading patterns are not confused with actual bird movements (Fudickar et al. 2012). In this initial phase, we applied only one decision rule to each individual's movement data: all sunrises not preceded by 4 or more hours of darkness were excluded. In a second phase, we applied a filter developed for use with satellite movement data (Gill et al. 2009), which limits daily movements based on two criteria—redundant distance and maximum speed. (Redundant distance refers to situations in which an individual is largely stationary and location readings on three consecutive days may have two locations in very close proximity to each other and one that is far-flung and likely in error; the redundant distance filter would catch this third location by analyzing the data set in three day increments and recognizing the one location that does not match the others.) We limited individuals to a redundant distance of 100 km and a maximum speed of 100 km h^{-1}.

Using this filtered movement data we identified arrival and departure dates for each stop for each individual. From these histories, we created year-specific population mean schedules with which we contrasted the movement history of each individual. We then determined whether each individual departed from the breeding grounds earlier or later than the mean population departure date and whether or not they became progressively earlier or later with each subsequent arrival or departure during the entire annual cycle.

FIGURE 3.1: Photo of attachment method of flags and BAS geolocation-tracking devices on adult Hudsonian Godwits. The logger is glued to the back of the alpha-alpha flag. See Figure 3.2 for a close up of attachment method. Photo Credit: Michael G. Harvey.

We created a series of sequential models to determine those variables that affect arrival and departure timing for each stage of the annual cycle. Each model included as its fixed-effects a set of variables representing the timing of those events that immediately precede it and individual as its random-effect variable. If a fixed-effect variable explained a significant portion of the variation in one model, it was carried to the next model. We considered the random-effects to have explained a significant amount of the variance in the model if two times the standard deviation for the random-effect was less than the estimated effect. Because random-effects determine the consistency of the effect of a variable on each individual, we concluded that the occurrence of significant random-effects in a model signified when specific individuals consistently deviated from the population mean timing for an event.

We monitored return rates of both logger and flag-carrying adults in subsequent years through daily observations at the breeding site and at adjacent feeding locations. Because we never recorded an individual returning after it was an absent for a year, we calculated return rates as the proportion of observed returning individuals versus the proportion of potentially returning individuals. To determine if carry-over effects might account for those individuals that did not return, we used a logistic regression to test if prior breeding success, number of nesting attempts, and accumulated lateness during the previous year affected the return rates of individuals carrying loggers. Similarly, we used a mixed-model logistic regression for all banded adults containing prior breeding success and number of nesting attempts as fixed-effects and individual as a random-effect to determine if either prior breeding success or the number of nesting attempts affected return rates in the wider banded population.

FIGURE 3.2: Attachment method of geolocation-tracking devices used on Hudsonian Godwits. A retrieved data logger is shown with the remnants of the flag with which it had been attached to the tibiotarsus of an adult godwit. To remove the flag from the godwit's leg upon retrieval, the "ring" encasing the leg had been cut away. Photo Credit: Andrew S. Johnson.

RESULTS

Individual godwits repeatedly made non-stop flights of longer than 10,000 km and 7 days during their northbound migrations and flights of longer than 5 days and 6,500 km during their southbound migrations (Figure 3.3). We found almost no inter-annual variation in migratory pathways — all but 2 of the 26 individuals stopped in the same suite of 6 regions each year (Figures. 3.3, 3.4).

We found little evidence that godwits maintain or accumulate delays across their annual cycle and no evidence that late-arriving individuals suffered reduced breeding success (Table 3.1). Certain events during the annual cycle did cause consistent deviations from population-average departure timing for some individuals (Figure 3.5, Table 3.1), which were characterized by significant random-effects but not fixed-effects — e.g., departure from the Amazon Basin (Individual random-effect variance, $\sigma^2 = 45.15$, $SD = 6.72$). Some other sites were consistently associated with increased delays, but for different individuals in different years (Table 3.1). These events — e.g., arrival on the breeding grounds (Average Stopover Duration, Estimate = 0.38, $SE = 0.11$, $t = 3.39$, $P < 0.05$; Number of Stops, Estimate = 2.06, $SE = 0.55$, $t = 3.71$, $P < 0.05$) — were characterized by significant fixed-effects, but not random-effects (Table 3.1).

Individuals did not continue to diverge from the population mean throughout the entire annual cycle because delays disappeared after specific "buffer events" (Figure 3.5). These buffer events — e.g., post-breeding staging in central Saskatchewan — were characterized by a lack of significant random- or fixed-effects (Table 3.1). As a result, individuals did not accumulate delays for longer than three events and accumulated lateness was not correlated with breeding success (Estimate = 0.03, $SE = 0.05$, $t = 0.60$, $P > 0.05$). The only variable tested that significantly affected breeding success was the number of nesting attempts undertaken by an

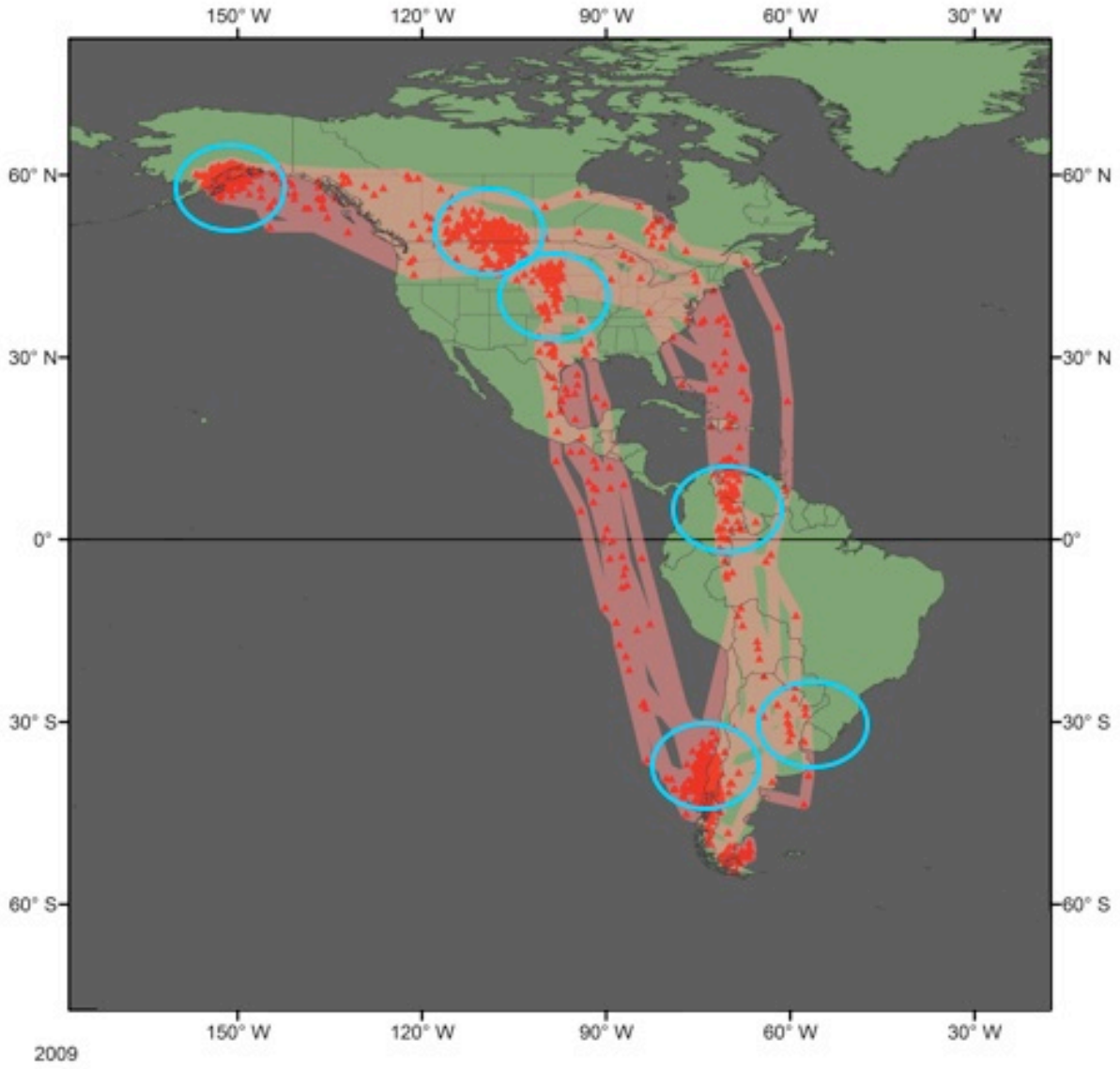


FIGURE 3.3: Migration routes of Hudsonian Godwits breeding at Beluga River, Alaska. Nineteen individuals were tracked across two years 2009-2011, though for ease of presentation this map only shows those from 2009-2010, using British Antarctic Survey Mk-14 geolocation-tracking devices. Each red triangle denotes the location of an individual on one day, but does not necessarily indicate that the individual stopped in that location. Each blue circle denotes a region in which the majority of godwits stopped and congregated in both years. From north to south, those regions are: Beluga River, Alaska (nesting site); central Saskatchewan; Rainwater Basin, Nebraska; Amazon Basin, Colómbia; Buenos Aires Province, Argentina; and Chiloé Island, Chile. Note that the typical migratory route is a clock-wise loop. See Figure 3.4 for order of usage within the annual cycle.

individual (Estimate = -0.46, $SE = 0.19$, $t = 2.47$, $P < 0.05$).

Potentially our data were biased by differences in return rates of bird such as lower return rates for birds that fell too far behind the optimal schedule. However, individual return rates were high in all years (82.7 ± 12.5% across all years) and individuals carrying data loggers returned at higher rates than did those individuals carrying only alpha-numeric flags (83.5 ± 10.0% vs. 80.9 ± 16.5% respectively, across all years). A logistic regression testing if prior breeding success, number of nesting attempts, and accumulated lateness during the previous year affected the return rates of individuals carrying data loggers was not a significant predictor of return rates and no single variable had a significant effect (Table 3.2). A mixed-model logistic regression for all banded adults also found that a model containing prior breeding success and number of nesting attempts was not a better predictor of return rates than a null model (ANOVA, df = 2, $P = 0.65$; Table 3.3).

TABLE 3.1: Model and parameter estimates for models explaining the variance in timing of events in the Hudsonian Godwit annual cycle (2009-2011). Bold-font variance and t-statistic values were determined to be significant at $P < 0.05$.

Model	Parameters	Random Effects			Fixed Effects			
		K	σ^2	St. Dev.	Variable	β	SE	*t*
Departure from Beluga River	Prior Breeding Success + Prior # Nests	Ind.	2.38	1.54	Intercept	-5.39	3.21	-1.68
					PBS	2.91	2.00	1.45
		Res.	33.94	5.83	P#N	3.42	2.06	1.66
Arrival in Sas.	Beluga Departure	Ind.	1.60	1.27	Intercept	0.33	0.30	1.10
		Res.	1.34	1.16	BRD	0.01	0.03	0.32
Sas. Depart.	Sas. Arrival	Ind.	3.47	1.86	Intercept	-0.15	1.09	-0.14
		Res.	53.82	7.34	SAA	-0.13	0.67	-0.20
Arrival in Amazon	Sas. Depart.	Ind.	0.00	0.00	Intercept	0.10	0.39	0.25
		Res.	8.08	2.84	SAD	-0.07	0.05	-1.28
Departure from Amazon	Amazon Arrival	Ind.	**45.15**	**6.72**	Intercept	0.31	1.70	0.18
		Res.	47.52	6.89	AMA	-0.59	0.38	-1.53
Arrival in Buenos Aires	Amazon Departure	Ind.	0.03	0.17	Intercept	0.57	0.28	2.00
		Res.	3.83	1.96	AMD	-0.03	0.03	-0.83
Departure from Buenos Aires	Arrival in Buenos Aires	Ind.	**28.01**	**5.29**	Intercept	0.76	1.79	0.43
		Res.	79.42	8.91	BAA	-0.47	0.74	-0.63
Arrival in Chiloe	Buenos Aires Departure	Ind.	1.27	1.13	Intercept	-0.41	0.67	-0.61
		Res.	18.47	4.30	BAD	-0.02	0.06	-0.34
Departure from Chiloe	Arrival in Chiloe	Ind.	**36.34**	**6.03**	Intercept	1.08	2.15	0.51
		Res.	115.15	10.73	CHA	0.83	0.42	1.98
Arrival in North America	Chiloe Departure	Ind.	0.00	0.00	Intercept	0.12	0.16	0.78
		Res.	1.06	1.03	CHD	-0.01	0.01	-0.88
Arrival in Beluga River	N.A Arrival + #Stops + Avg. Stop. Duration + # Nests	Ind.	1.53	1.24	Intercept	-8.35	2.23	-3.74
					NAA	-0.28	0.34	-0.82
		Res.	3.44	1.85	**Stops**	**2.06**	**0.55**	**3.72**
					ASD	**0.38**	**0.11**	**3.39**
Breeding Success	Beluga River Arrival + #Stops +Avg. Stop. Duration + # Nests	Ind.	0.00	0.00	Intercept	1.55	1.00	1.55
					BRA	0.03	0.05	0.60
		Res.	0.20	0.44	Stops	-0.14	0.31	-0.44
					ASD	-0.03	0.04	-0.73
					#Nests	**-0.46**	**0.19**	**-2.47**

DISCUSSION

This is the first study to document how individuals of a migratory species accrue and dissipate delays across multiple stages of the annual cycle. We found that in spite of having one of the most extreme migrations of any migratory bird, returning godwits that fell behind during one portion of their annual cycle did not subsequently fall further behind during the remainder of their annual cycle, nor did they suffer reduced breeding success. Authors of recent studies have marveled at the marathon distances traveled in non-stop migratory flights by some migrants (Gill et al. 2009), but also at the consistency of arrival and departure dates of individuals and the lack of apparent carry-over effects within some species (Battley 2006, Conklin and Battley 2011, Lourenço et al. 2011, Conklin and Battley 2012). Buffer events — which we define as annual-cycle events when resources (food or time) are so abundant that all individuals are able to alleviate stress (lateness) that they have accumulated during previous portions of their annual cycle — may explain these seemingly contradictory observations. Long-distance migrants, and especially Arctic breeders, incur significant amounts of stress throughout their annual cycle, with much of it coming during acute episodes such as long, non-stop flights or incubation during near-freezing conditions (Battley et al. 2000, Guglielmo et al. 2001, Reneerkens et al. 2002, Piersma et al. 2003, Buehler et al. 2010). Having sites that provide the resources capable of limiting the accumulation of these stresses may be critical to the success of such extreme life-history strategies, especially over the course of the long lifespan of many of these species (Colwell et al. 1995). We suggest that buffer events should be considered on the same level of importance within the annual cycle as the more traditional components of breeding, molt, and migration (Buehler and Piersma 2008).

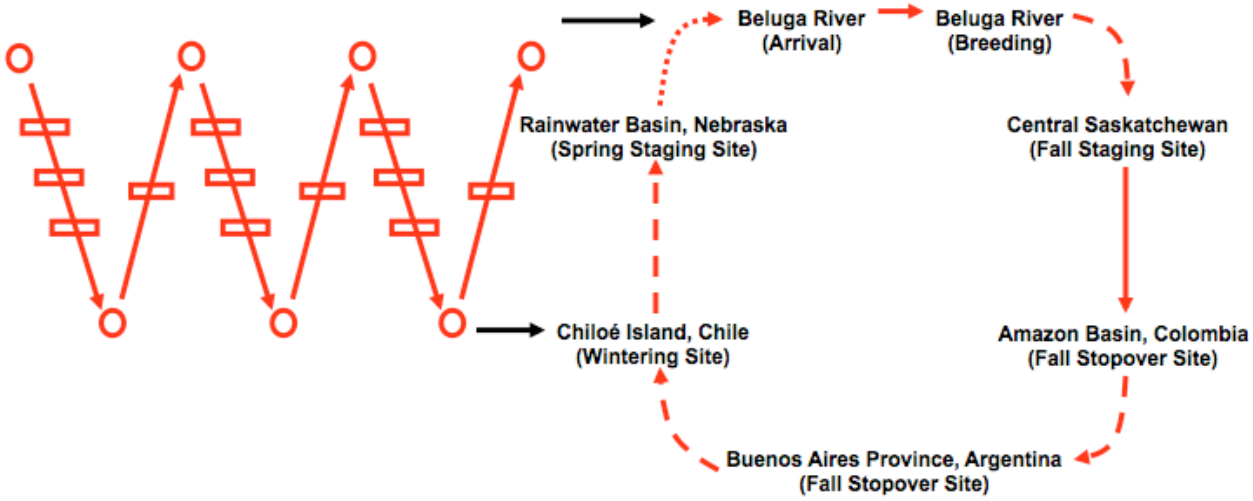


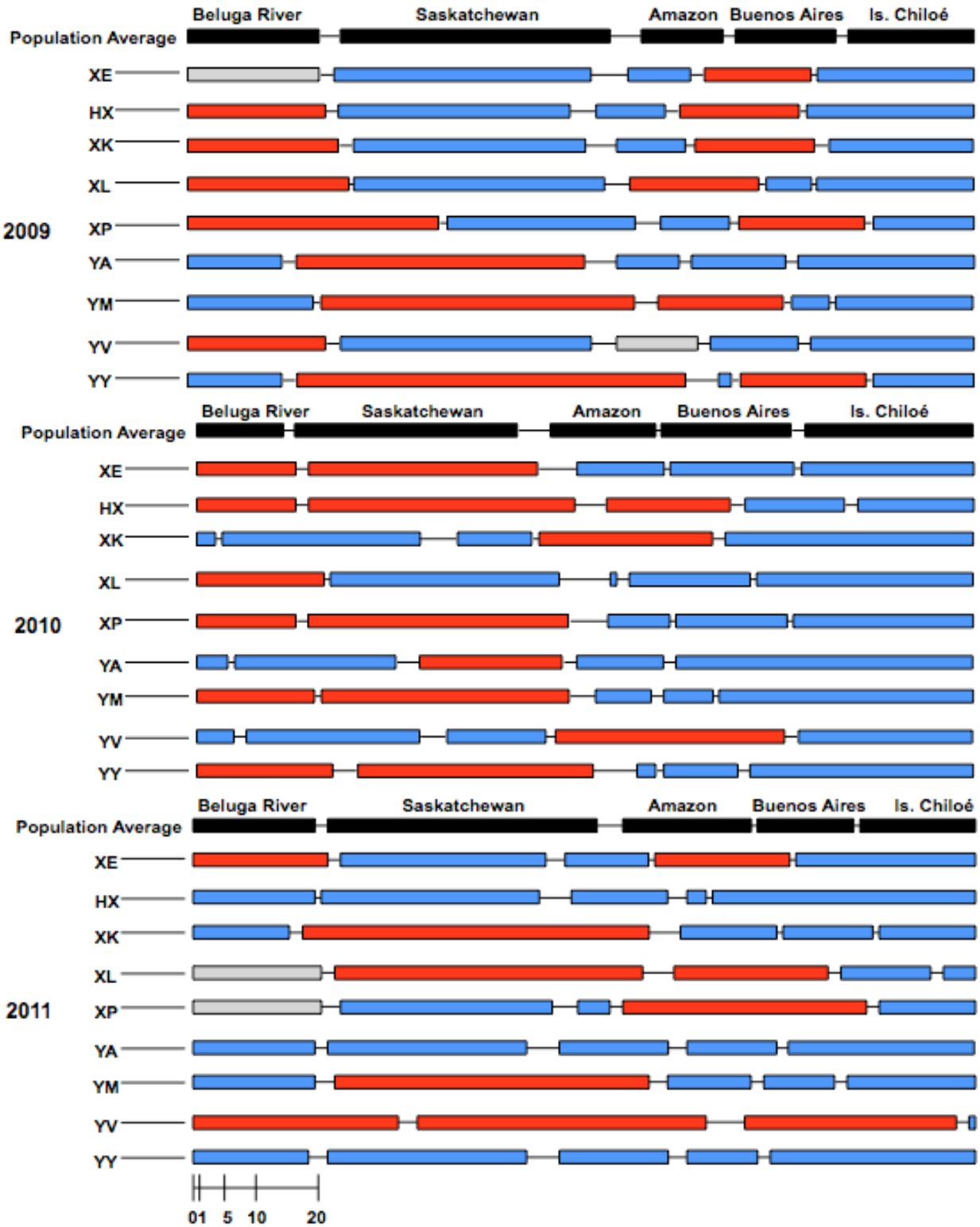
FIGURE 3.4: Annual cycle of Hudsonian Godwits and the creation and persistence of carry-over effects. On the left is a schematic representing the period of time (2009-2012; 4 breeding seasons and 3 complete migrations, with 4 stopover or staging sites annually) that our study covers. On the right, the schematic cycle denotes the sequence of events within one full annual cycle. Arrows denote travel events (generally, continuous flights) between named locations. The named locations denote stopover events whose duration may be affected by carry-over effects from previous events. The presence or absence of carry-over effects is denoted by the type of line connecting each pair of events. Events not linked by carry-over effects are indicated by a solid line, events associated with inter-annually consistent deviations in timing among individuals are indicated by dashed lines, and the event affected by non-individually consistent deviations is indicated by a dotted line.

Types of Annual-Cycle Events

We found three different types of events during the godwit annual cycle: 1) Some events during stressful periods of the annual cycle, such as departure from the breeding grounds and stopovers following long, non-stop flights, consistently caused some individuals to begin to accumulate lateness compared to the population average (Figure 3.5). Owing to the consistent manner with which individuals responded to these stresses, we surmise that these deviations resulted from carry-over effects caused by differences in intrinsic individual quality. 2) Other events caused timing delays, but did so for different individuals in each year. For instance, those individuals that stopped more often during their northward migration and stayed at stopover sites longer also arrived later on their breeding grounds, but few individuals were delayed in the same manner in all three years (Table 3.1). Because these deviations were not individually consistent, we concluded that these carry-over effects were likely caused by extrinsic events, such as poor weather conditions during migratory flights. 3) Finally, buffer events preceding or subsequent to stressful portions of the annual cycle alleviated the lateness that had accumulated during previous events and allowed individual godwits to realign the timing of their movements with the population mean.

Buffer events change our understanding of how migratory birds organize their annual cycle, by altering the way we think about trade-offs in resource allocation. For example, an individual's decisions related to competition for limited resources (Kokko 1999, Kokko et al. 2006) are traditionally viewed within the context of resource allocation over the life span of an individual — if an individual expends too much energy during one season in order to secure its share of limited resources, it may never recoup those resources or it may suffer reduced fitness during subsequent seasons (Norris 2005, McNamara and Houston 2008). Our results suggest that

FIGURE 3.5: Deviations in timing from the population mean by nine individual Hudsonian Godwits tracked during southward migration for three consecutive years, 2009-2011. Each bar denotes the number of days spent at a site and lines between bars the number of days spent traveling between sites. Red bars identify sites at which individuals accumulated delays; blue bars those sites at which they began to erase these delays; gray bars those sites at which they neither became earlier nor later. The population average schedule is shown at the top of the figure in black.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Amazon
Buenos Aires
Is. Chiloé
Population Average
XE
HX
XK
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XP
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YM
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Beluga River
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resource allocation decisions are instead made by godwits on a shorter time scale. Godwits may be able to expend a tremendous amount of energy completing an event (i.e. breeding or migration), so long as they maintain sufficient energy to survive until they reach a buffer event site. Consideration of resource allocation on such a time scale means that what is optimal for one species (or population), may not be necessarily optimal for all species (McNamara and Houston 2008).

Conservation Implications

The existence of buffer events has important conservation implications. Specifically, the quality of sites at which buffer events occur (in the godwits' case, organically supra-abundant mudflats) is vulnerable to degradation from human impacts. After a certain point, site quality can be degraded to such an extent that these sites can no longer act as buffers against accumulating stress, and serve instead simply as stopover or staging sites. This would be an important distinction, because staging and stopover sites are considered important only in the context of what event immediately preceded the site and what event immediately follows the site (Buehler and Piersma 2008, Warnock 2010). For instance, godwits stop in both the Amazon Basin and Buenos Aires during their southbound migration after four-six days of non-stop flying and must refuel for subsequent multi-day flights at these locations. However, individuals still accumulated lateness during their use of these sites. Buffer events, instead, are periods during which resources (food or time) are in sufficient excess to allow an individual to accomplish everything that must be done to not only prepare for the future, but also to overcome past stress that may have accumulated over multiple stages of the annual cycle. Godwits leaving buffer-event sites in central Saskatchewan have not accumulated additional lateness and, in fact, have alleviated the lateness with which they arrived. Degrading the quality of these buffer-event sites would likely

entail that stress could accumulate unabated for godwits from their departure on northbound migration in April through to their arrival, again, at non-breeding sites the following November. Buffer events therefore not only serve as a transition period between two consecutive events during the annual cycle (i.e., a staging site), but as a buffer among events occurring throughout the annual cycle. While low-quality individuals may always become delayed during stressful portions of their annual cycle, degrading buffer-event sites could affect all individuals within a population, regardless of their intrinsic quality.

Most migratory species must currently contend with environmental degradation during portions of their annual cycle and examples of carry-over effects involving other long-lived species, such as red knots, *Calidris canutus rufa*, and Icelandic black-tailed godwits may manifest the consequences of buffer-event site degradation (Gunnarsson et al. 2005, Baker et al, 2004). In our study system, decreasing the quality of fall staging sites in central Saskatchewan or non-breeding sites on Chiloé Island could have significant detrimental impacts on the entire annual cycle of Hudsonian Godwits. Prioritizing the protection of these sites may disproportionately increase the positive effect of conservation actions (Sheehy et al. 2010, Warnock 2010).

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TABLE 3.2: Factors affecting the return rates to their breeding grounds of Hudsonian Godwits carrying data loggers, 2010-2011. Parameter estimates for a linear mixed-model predicting breeding ground return rates of individual godwits carrying data loggers. (n = 18)

Random-Effects			
Variable	**Variance**	**Standard Deviation**	
Individual	2.43×10^{-3}	0.49	
Year	4.13×10^{-10}	2.03×10^{-5}	
Fixed-Effects			
Variable	**Estimate**	**Standard Error**	**P-value**
Intercept	25.04	2.24×10^{7}	1.00
Previous Breeding Success	-1.62	4.82×10^{5}	1.00
Previous Number of Nesting Attempts	3.59	2.23×10^{7}	1.00
Accumulated Lateness	0.14	100.61	0.99

TABLE 3.3: Factors affecting breeding ground return rates of all banded Hudsonian Godwits, 2010-2011. Parameter estimates for a mixed-effect logistic regression model predicting breeding ground return rates of individual godwits carrying data loggers. (n = 73)

Random-Effects		
Variable	**Variance**	**Standard Deviation**
Individual	7.9×10^{-10}	2.81×10^{-5}
Data Logger	1.34×10^{-12}	1.16×10^{-6}
Year	0.37	0.61

Fixed-Effects			
Variable	**Estimate**	**Standard Error**	**P-value**
Intercept	0.28	1.07	0.79
Previous Breeding Success	0.96	1.54	0.12
Previous Number of Nesting Attempts	1.03	0.84	0.22

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CHAPTER 4

WHY STOP? CAUSES AND CONSEQUENCES OF UNEXPECTED STOPOVERS IN A MIGRATORY BIRD

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ABSTRACT

Global climate change is altering not only mean weather and climatic conditions, but also the incidence and frequency of extreme weather events. These simultaneous changes present challenges to organisms across trophic levels because they can absorb much of the flexibility present in a species' annual cycle. Such hurdles may be especially great for migratory species having precisely timed events during their annual cycle that are spread widely across the globe and separated by multiple climate change regimes. We explore how changes in mean environmental conditions on the breeding grounds and occurrence of stochastic weather events during migration combine to affect the breeding success of a long-distance migratory bird, the Hudsonian Godwit, *Limosa haemastica*. Occurrence of strong headwinds and low pressure systems associated with storm tracks can cause migrating godwits to make use of unexpected stopover sites. Unexpected stops delay arrival on the breeding grounds, but currently do not affect reproductive success. Future climatic changes are projected to disrupt godwit migrations through changes in wind patterns and occurrence of droughts. Under such conditions godwits may be forced to make unexpected stops more frequently, leaving them vulnerable to delays sufficiently large to affect reproductive timing and success.

INTRODUCTION

Global climate change is altering climate and weather conditions in myriad ways, mostly falling into two broad categories: changes in the overall mean conditions in a region and changes in the frequency of occurrence of extreme weather events (Canale and Henry 2010). The effects of these two types of climatic change on organisms are very different, but many organisms are being subjected simultaneously to both types of change (Parmesan et al. 2000). Our understanding of how organisms will react to these changes is still in its infancy, but a growing body of literature explores how organisms are responding to gradual climatic changes (Forrest and Miller-Rushing 2010) and, separately, how they respond to rapid, dramatic changes (Canale and Henry 2010). How the ability of an organism to respond to one type of change may influence its ability to adapt to the other remains little explored.

A fundamental challenge facing migratory species is timing their movements from their wintering areas to their breeding grounds so as to coincide with the availability of the resources needed to raise young (Durant et al. 2007). Properly timing their movements is made more difficult by global climate change: spring is accelerating across much of the northern hemisphere, but is doing so asynchronously in different regions, challenging some species to speed up their migration, but also to reconcile conflicting climate change regimes (Jones and Cresswell 2010). Some populations may be able to respond to these types of climatic changes, so long as the cues that they use to time the events in their annual cycle remain reliable (Love et al. 2010, Chapter 1). Other populations, now faced with unreliable cues, are becoming mismatched with local food resource phenology and suffering breeding failures and population declines (Both 2010, Chapter 2).

Stopover sites during northward migration are critical to the timing of the annual cycles

of migratory birds (Alerstam and Lindström 1990). Under optimal conditions, stopover sites offer migratory birds opportunities to rest and refuel in between migratory flights (Senner 1979). They can also allow migrants to wait for the onset of proper conditions (e.g., warming temperatures) at more northerly sites before continuing with their migration (Bauer et al. 2008). Optimally, migrating birds make stopovers when fuel stores are running low or when high-quality habitat is available (Alerstam et al. 2003) and, over time, the confluence of physiology and habitat availability have led to the evolution of stable suites of stopover sites for many species (Warnock and Bishop 1998). However, under sub-optimal conditions such as poor pre-migratory fueling or adverse weather conditions, migrants may be forced to stopover at non-traditional sites that may occur in poor resource environments (Shamoun-Baranes et al. 2010).

Because of the importance of stopover sites for the timing of migratory annual cycles, storms and other extreme weather events can affect the ability of migratory species to time their migrations optimally, both on an annual and interannual basis (Alerstam et al. 2003). In the short term, an ill-timed storm may delay an individual or even a population, causing late arrival on the breeding grounds and potentially a mistimed breeding effort (Kokko 1999, Newton 2006). In the longer term, increased frequency of severe weather events or changes in the location of storm tracks could alter the ability of populations to complete their migrations (Gill et al. 2009) or to respond to other simultaneous climatic changes (Canale and Henry 2010). Beyond these generalities, however, little is known about how such weather events affect the migrations of individuals and populations or how these may affect the ability of populations to respond to other climatic changes (Piersma and Lindström 2004). Given the predicted increase in extreme weather events and movement of storm tracks in the next century, specific information about how long-distance migrants handle unpredictable weather events will allow for an accurate

assessment of the future health of these populations (Klaassen et al. 2012).

Here we examine how stochastic weather events affect a long-distance migratory bird, the Hudsonian Godwit, *Limosa haemastica*, on its northward migration from southern Chile to sub-arctic Alaska. We identify those events that cause individual godwits to make unexpected stops at non-traditional stopover sites during their migration and how these stops affect the timing of their arrival on the breeding grounds and subsequent breeding success. We apply these findings generally to predictions of future climate change scenarios, and project how the hemispheric migrations of godwits and other species may be altered by future changes.

METHODS

Study Species

Hudsonian Godwits (hereafter, godwits) nest in three disjunct populations across the Nearctic of Alaska and Canada—the western Hudson Bay lowlands, Arctic northwestern Canada and northeastern Alaska, and southcentral and western Alaska. These three populations correspond, respectively, to three separate wintering populations in southern South America—1) bahías Lomas and San Sebastián on Tierra del Fuego, Bahía Samborombón in the Buenos Aires province of Argentina, and Isla Chiloé in southern Chile (Walker et al. 2011). Godwit migration involves long, non-stop flights of more than 10,000 km, punctuated by lengthy stopovers in a few traditional regions. Our study population — the southcentral and western Alaska breeding population (hereafter, Alaskan population) — generally makes use of only six regions during its entire annual cycle and only three during their northward migration: Departing from Isla Chiloé in early April, godwits fly non-stop to the central United States, with most individuals stopping only once, in the central Great Plains of Kansas and Nebraska for as long as three weeks, before

again flying non-stop to their breeding grounds in Alaska, where they arrive by the first few days of May (Chapter 3). Occasional stops at intermediate, and apparently unexpected, stopover sites do occur among a few individuals and can delay the arrival of individuals at breeding sites (Chapter 3). Additional stops are not made consistently by certain individuals between years, but may be caused either by poor pre-migratory fueling or by sub-optimal or extreme weather conditions experienced *en route* (Shamoun-Baranes et al. 2010, Chapter 3).

Migration Tracking

We placed British Antarctic Survey Mk-14 and Mk-10 geolocation-tracking devices (hereafter, loggers) on 79 breeding adult godwits at Beluga River, Alaska (61.21°N, 151.03°W) in three successive breeding seasons, 2009-2011. We attached loggers to a uniquely coded alpha-alpha flag placed on the left upper tibia and separated from the tibio-tarsal joint by a UV-resistant color band to reduce potential wear on the joint. Mk-14 and Mk-10 loggers weigh 1.4 or 1.1 g (depending on year), roughly 0.44-0.56% of mean godwit lean mass (Walker et al. 2011). Upon recapture during subsequent years after marking, logger-bearing flags were removed from the legs of godwits and new logger-bearing flags were attached to replace them.

After retrieval, we downloaded and initially analyzed movement data using BAS software (version 8, March 2010). BAS loggers measure ambient light levels once per minute and record the maximum light level occurring every 5 minutes throughout the deployment of the logger. Light level information is transformed to identify the timing of sunrise, sunset, and solar noon for each day of deployment, which is, in turn, used to calculate the approximate twice-daily (noon and midnight) locations of loggers. The precision and accuracy of locations given by this method can be limited (Lisovsky et al. 2012). We therefore applied decision rules to the raw movement data so that errors caused by unusual shading patterns (e.g., heavy cloud cover) were

not confused with actual bird movements (Fudickar et al. 2012). In the initial phase, we removed all locations corresponding to (apparent) sunrises not preceded by 4 or more hours of darkness. In a second phase, we applied a filter developed for use with satellite movement data, which limits daily movements based on two criteria — redundant distance and maximum speed (Gill et al. 2009). (Redundant distance refers to situations in which an individual is largely stationary and location readings on three consecutive days may have two locations in very close proximity to each other and one that is far flung and likely in error; the redundant distance filter would identify the erroneous location by analyzing the data set in three day increments and recognizing the one location that does not match the others.) We limited individuals to a redundant distance of 100 km and a maximum speed of 100 kmh^{-1}.

Finally, we divided the northward Alaskan godwit migration route into 45 grid cells (Figure 4.1). Grid cell sizes were chosen corresponding to the frequency with which godwits stopped in the region: regions with more godwits stopping-over were more finely sub-divided so as to facilitate a more precise estimation of the conditions leading to stopover decisions. Each of an individual godwit's twice-daily (filtered) locations was then assigned to one of these grid cells so that the godwit's position could be aligned with weather, climate, and habitat data corresponding to that grid cell. We considered an individual to have stopped when two consecutive locations were spaced by less than 1º longitude (Schmaljohann et al. 2012). Stopovers were assigned to grid cells using the mean latitude and longitude of locations recorded during the stopover period.

Unexpected and Expected Stops

Our preliminary analysis determined that many godwits stopped over only in a small region in the northcentral coterminous United States roughly bounded by central Kansas and southern

South Dakota. To quantify the bounds of this core region and determine what proportion of individuals stopped there, we used a utilization distribution kernel analysis that included all raw location estimates for each migrating godwit from 2009-2011 during the month of April occurring north of 12°N and east of 125°W. For this analysis we used a 100 km grid and a 250 km smoothing parameter (*h*) with the "kernelkcbase" function in the "adehabitat" library in program R (ver. 2.10.1; R Development Core Team 2009). In total, 49% of all stops occurred within a core region that corresponded to the 75% distribution kernel, meaning that 75% of all location estimates during the migration period occurred within this region (Figure 4.1). The remaining 51% of stopovers occurred at scattered places throughout the rest of the migration corridor. We termed those stops that occurred within the core region "expected" stops, as every godwit stopped inside this core region, regardless of whether they also stopped outside of it. Those that occurred outside of the core region we termed "unexpected" stops.

Breeding Success

Methods for monitoring breeding success have been described in more detail in Chapters 2 and 3. Briefly, we monitored adult godwits from their arrival at the Beluga River breeding site through their departure following the breeding season. We discovered nests using behavioral cues or by opportunistically flushing incubating individuals and determined the number of nesting attempts made by an individual by monitoring each nest every 2-3 days until the nest had either failed or hatched. Upon hatch, we captured all chicks in a brood before they left the nest. Godwits fledge at the age of 28 days (Walker et al. 2011) and once the earliest chicks to hatch had potentially reached this age, we surveyed our study site daily for fledged chicks. We denoted an individual adult as having bred successfully if at least one chick from its brood reached an age of 28 days.

Statistical Analysis

We developed six hypotheses that could potentially determine what causes an individual bird to use an unexpected stopover site during its northward migration, each with a discrete set of predictions (Table 4.1). To test these hypotheses, for the 1 Apr-10 May migration period, we gathered daily temperature and precipitation conditions aligned with each grid cell from the North American Regional Reanalysis (Mesinger et al. 2006), eight times daily wind conditions from the R package RNCEP (Kemp et al. 2012), and daily soil moisture measurements — as an index of the availability of wetland habitat at stopover sites — aligned with each grid cell from the University of Washington Experimental Surface Water Monitoring database (Wood 2008). All of these conditions could significantly affect an individual's choice of stopover sites, number of stops made, and duration of migration (Åkesson and Hedenström 2000, Bauer et al. 2008, Skagen et al. 2008).

TABLE 4.1: Hypotheses and predictions related to the conditions causing migratory birds to make use of stopover sites during their migration.

Hypothesis	**Description**	**Prediction**
Extreme Weather	An individual encounters an extreme weather event	Weather conditions on the day a stop is made will be best predictor of stopover decisions
Random Events	An individual has poor pre-migratory fueling or is intrinsically low quality	None of the environmental conditions will reliably predict stopover decisions
Habitat availability	Habitat availability at a non-traditional stopover is high or habitat availability at a traditional stopover site is low	Soil moisture levels at non-traditional stopover sites will be best predictor of stopover decisions
Past Habitat Availability	Habitat availability along the migration route is weighted by previous experience.	Long-term mean soil moisture levels will be the best predictor of stopover decisions.
Approaching Conditions	Conditions further along the migration route are sub-optimal, such as sub-zero temperatures	Weather conditions in the grid cell immediately north of a stopover site will be best predictor of stopover decisions
Accumulation of Poor Conditions	An individual experiences consistent, but not extreme, headwinds during their flight	Cumulative real distance traveled will be the best predictor of stopover decisions

Wind is frequently considered to be one of the most important factors determining the speed, duration, and energy involved in long-distance bird migration (Åkesson and Hedenström 2000). Nevertheless, empirically measuring the real effect of wind on migrating birds in flight has proven difficult. Given the distances traveled by godwits in non-stop flights, wind presumably plays an especially important role in determining the rate of their migrations and the number of stops made. Therefore, including wind in our analysis was critical to evaluating godwit stopover decision-making process. To calculate how much hindrance or assistance an individual received from wind during its flight, we estimated the air distance (AD) covered by each individual. To estimate AD, in addition to the ground distance (GD), covered by an individual, we assumed that the speed of an individual in the air (AS) was stable during each time interval (time between two consecutive location fixes), but that ground speed (GS) changed because of wind. AD in this case can be estimated from AS:

$$AD=AS\times Time$$

To get AS, the following integral should be solved:

$$GD=\int Speed(time)dtime$$

or

$$GD=\int (AS+TailWind(time))dtime$$

We then estimated AS by iteratively solving this integral and minimizing the difference between real and estimated GD. Using winds measured every three hours at 925 mb (Shamoun-Baranes et al. 2010) from along the measured flight path of an individual and accessed through the RNCEP portal (Kemp et al. 2012), this process resulted in an estimated real speed (kmh^{-1}) for each 12-hour time segment on a continuous flight. We converted this real speed to a distance (km) and subtracted it from the measured ground distance from the same segment, to arrive at a

comparative measurement of real distance covered. A negative distance for a twelve-hour segment meant that an individual benefited from a tail wind and "traveled" less far than in still air, as the tail wind enabled it to use less energy per unit of ground distance covered. Conversely, a positive distance meant that an individual had flown into a headwind and traveled farther than in still air and used more energy per unit of ground distance covered.

In order to link the other environmental conditions experienced by migrating individuals to stopover decisions, conditions occurring in every grid cell traversed along an individual's flight path each day were recorded (see Table 4.2 for a list and description of all variables). "Approaching conditions" were taken from the next grid cell along an individual's flight path extended beyond its last measured location for a given day. Air pressure co-varied strongly with latitude ($r = 0.97$), so we regressed air pressure against latitude and used the residuals from this regression in all analyses.

The one potentially important component missing from our analysis was body mass at departure from the non-breeding grounds and subsequent stopover sites. Work with Bar-tailed Godwits, *Limosa lapponica baueri*, and other long-distance migratory shorebirds has shown that an individual's body mass, and related body fat content and flight muscle size, at departure are critically important to the distance it is capable of covering during a migratory flight and, presumably, its likelihood of stopping unexpectedly (Battley and Piersma 2005). These data are unavailable for Hudsonian Godwits and we recognize this limitation. By using repeated measurements for a suite of individuals and a mixed-model analysis framework, we do, however, account for individual variation and the possibility that some low quality individuals could employ a migration strategy characterized by more frequent stops (but see Chapter 3).

We conducted a three-stage analysis to determine how weather and climate affect godwit

stopover decisions and how the number of stops made affected both arrival date on the breeding grounds and breeding success. In the first stage, we identified differences between days on which godwits stopped and days on which they continued flying. Secondly, we identified differences between days on which godwits stopped at traditional stopover sites and days on which they stopped at unexpected sites. Thirdly, we estimated the effect on arrival date and breeding success of the number of expected and unexpected stops made by an individual, as well as its cumulative real distance flown.

For the initial logistic regression analysis, each day during an individual's northward migration from its non-breeding to breeding sites was coded in one of three ways: 1) Days in which an individual flew continuously without stopping (regardless of whether or not it began its flight that day); 2) Days in which an individual stopped after having been in flight; and 3) Days in which an individual did not fly or could not have stopped because the entirety of its flight took place over open ocean. Days in this third category were discarded from the analysis.

In addition to the six hypotheses listed in Table 4.1, we separately tested the effect of each variable on the likelihood that an individual stopped instead of continuing to fly in a Generalized Linear Mixed Model (GLMM) — with a binomial distribution, the environmental condition as a fixed effect, and Year, Individual, and Grid Cell as random effects. We included those variables that were independently significant predictors in a seventh hypothesis: a global "best" model. To compare among the hypotheses, we included each environmental variable in at least one of seven separate models, one for each hypothesis. We fitted the models using a GLMM with a logit link function and binomial error distribution, where days on which an individual stopped were coded as "1" and days on which it flew continuously were coded as

TABLE 4.2: Description of all environmental conditions included as variables in analyses of the causes of stopovers during Hudsonian Godwit migration 2010-2012.

Variable	Description	Hypotheses
Headwind	Calculated from the flight heading of an individual and the direction and magnitude of winds encountered in all grid cells flown through during a given day.	Extreme Weather, Global Best
Maximum Wind	Maximum wind speed encountered amongst all grid cells flown through on a given day	Extreme Weather, Global Best
Next Wind	Wind speed in next grid cell along flight path given a day's flight heading	Approaching Conditions
Next Headwind	Calculated headwind in next grid cell along flight path given a day's flight heading	Approaching Conditions
Temperature	Mean daily temperature in the last grid cell encountered during a day's flight	Extreme Weather
Next Temperature	Mean daily temperature from the next grid cell along flight path given a day's flight heading	Approaching Conditions
Residual Air Pressure	Residual air pressure in the last grid cell encountered during a day's flight	Extreme Weather, Global Best
Next Residual Air Pressure	Residual air pressure from the next grid cell along flight path given a day's flight heading	Approaching Conditions
Cumulative Real Distance Flown	Difference between real distance flown and ground distance added over all previous days of flight	Accumulation of Poor Conditions, Global Best
Cumulative Distance	Total ground distance covered during all previous days of flight	Accumulation of Poor Conditions
Distance Since Last Stop	Total ground distance covered during all flights following previous stop	Accumulation of Poor Conditions
Long-term Mean Soil Moisture Level	Long-term mean soil moisture level for last grid cell encountered during a day's	Past Habitat Availability

Variable	Description	Hypotheses
	flight	
Average Long-term Mean Soil Moisture Level	The average long-term mean soil moisture level amongst all grid cell encountered during a day's flight	Past Habitat Availability, Global Best
Soil Moisture Level	Current soil moisture level of the last grid cell encountered during a day's flight	Current Habitat Availability
Soil Moisture Anomaly	Soil moisture anomaly of the last grid cell encountered during a day's flight and calculated based on the long-term mean soil moisture level for that grid cell on that day	Current Habitat Availability
Average Soil Moisture Level	Average current soil moisture level amongst all grid cells encountered during a day's flight	Current Habitat Availability, Global Best

"0"; Year, Individual, and Grid Cell were random effects; and the environmental conditions were fixed effects. We then selected the best models using Akaike's Information Criterion (Burnham and Anderson 2001).

In the second step of the analysis, we tested for differences among days on which individuals stopped in expected and unexpected locations. We then repeated the GLMM analysis using the same seven models as in the first stage of the analysis, although in this case, unexpected stops were coded as "1" and expected stops "0", and again selected the best models using Akaike's Information Criterion.

In the third step of the analysis, we tested for the effects of the number of total and unexpected stopovers made en route on arrival date and breeding success using separate GLMMs. Individual and Year were again included as random effects and the breeding success model was tested with a logit link function and binomial error distribution.

To complete the analysis, we tested for geographic and intraseasonal trends in three important environmental conditions that were correlated with stopovers: headwind, air pressure, and soil moisture levels. Using the results from the three-step logistic regression analysis, we identified headwinds and air pressures that corresponded with days on which godwits stopped in unexpected locations. For headwinds, we then used the mean heading of godwits migrating through each grid cell to calculate daily headwinds and then to count the number of days in each year and grid cell during which a migrating godwit would have encountered a significant headwind. We similarly tallied days on which air pressures dropped below the threshold

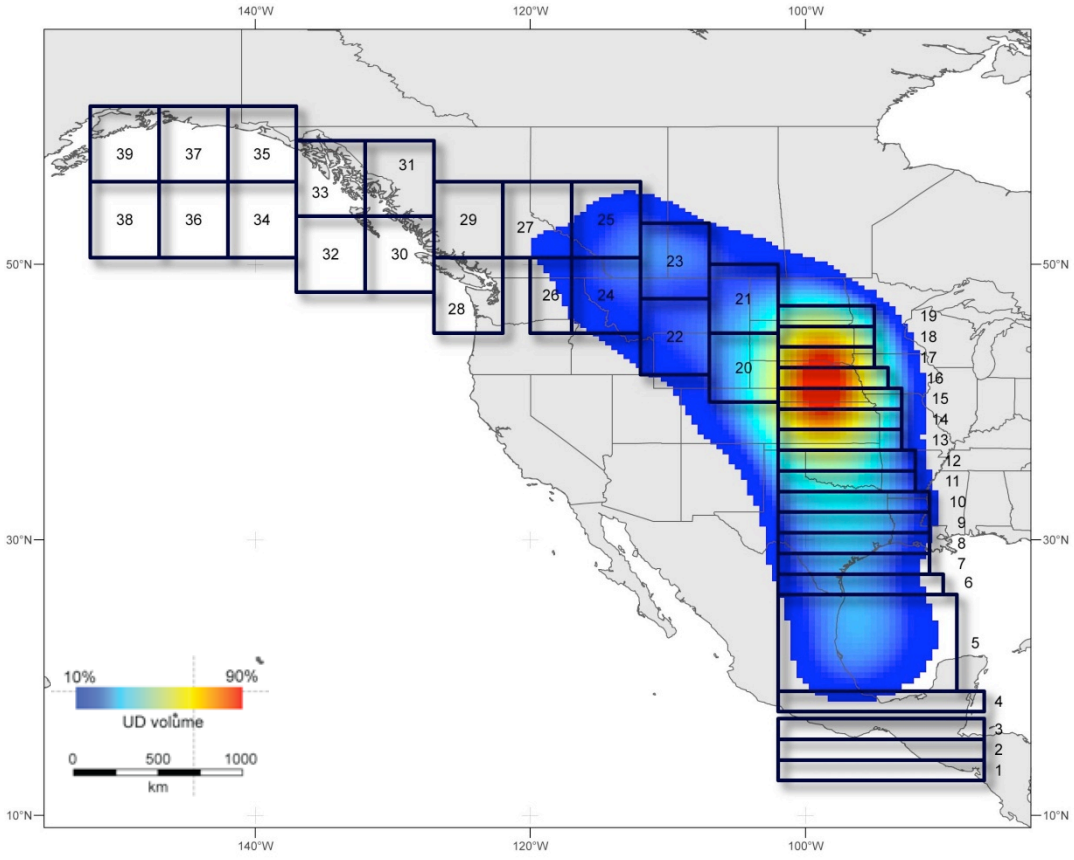

FIGURE 4.1: Distribution of Hudsonian godwits in April 2010-2012 during northward spring migration from South America to their breeding grounds in Alaska. Maps show kernel home range utilization distributions (UD) derived from April location estimates that were north of 12°N and east of 125°W. Grid cells displayed are those used for aggregating all environmental variables used in subsequent analyses.

causing godwits to stop. Finally, we estimated long-term mean soil moisture levels from each grid cell, using daily interpolations of data taken from 1916-2008. We used these three counts in GLMMs to test for geographical (by grid cell) and temporal (daily and yearly) differences in the likelihood of experiencing adverse conditions. (All analyses were done using the "glmer" function in the "lme4" library in Program R; ver. 2.10.1; R Development Core Team 2009).

RESULTS

Godwit Migration

We recovered 55 geolocators (69% recovery rate) from 28 individuals over three years, yielding 41 full and 3 partial sets of migration tracks from 21 individuals for this study. Fourteen of these individuals were tracked for multiple years, including eight for all three years. Godwits departed non-breeding sites on 6 April ± 0.43 d and arrived at their breeding sites 1 May ± 0.53 d, for a mean migration duration of 25 ± 0.52 d (n = 41). Godwits traveled a mean distance of 15,456 ± 163 km and flew 9,861 ± 152 km before their first stop (with a maximum flight of 10,680 km); they stopped 2.36 ± 0.18 times for an average of 6.15 ± 0.54 d per stop (n = 99). They stopped 1.05 ± 0.05 times per year in expected grid cells for an average of 9.53 ± 0.81 days per stop (n = 47; two loggers stopped working in the middle of the stopover period) and 1.32 ± 0.18 times per year in unexpected grid cells for an average of 2.98 ± 0.33 d per stop (n = 50). All godwits made at least one stopover. If an individual only made one stopover, it was always in an expected grid cell (n = 11).

Causes of Stopover Decisions

Godwits had 328 flight days during which an individual could have stopped. On 99 of those days, they stopped, and on the remaining 229 they flew continuously. The models representing

the seven hypotheses explaining the causes of stopovers had significantly different explanatory capabilities (Table 4.3). The minimum AIC model was the Global model (w_i = 0.99), which contained variables for cumulative real distance flown and its quadratic term, long-term mean soil moisture levels, residual air pressure and its quadratic term, headwind, maximum wind, and an interaction term between residual air pressure and headwind. The Past Habitat Availability model was second best, but was not well supported (ΔAIC = 21.7, w_i = 0.01). Among the variables included in the Global model, the interaction term between residual air pressure and headwind was the best predictor variable and had a negative relationship with the decision to keep flying ($\beta = -4.34 \times 10^{-3}$, SE = 1.83×10^{-3}, z = -2.38, P =0.02). Cumulative real distance flown was the second best predictor variable and also had a negative relationship with the decision to keep flying ($\beta = -1.07 \times 10^{-3}$, SE = 4.66×10^{-4}, z = 2.29, P = 0.02). Two other variables also had significant slope coefficients (residual air pressure and its quadratic term; Table 4.4).

TABLE 4.3: Model selection for the effects of environmental conditions on the use of stopover sites during the migration of Hudsonian Godwit, 2010-2012.

Model	**K**	**Deviance**	**AIC**	**ΔAIC**	w_i
Global	11	202.5	226.5	0	0.99
Past Habitat Availability	5	236.2	248.2	21.7	<0.01
Current Habitat Availability	6	234.5	248.5	22.0	<0.01
Random Events	3	344.0	352.0	125.5	<0.01
Approaching Weather	8	341.2	359.2	132.7	<0.01
Extreme Weather	8	344.5	362.5	136.0	<0.01
Accumulation of Poor Conditions	7	356.8	372.8	146.3	<0.01

TABLE 4.4: Model coefficients for factors explaining the use of stopover sites during the migration of Hudsonian Godwits 2010-2012. All environmental conditions are measured on a daily time scale. (Number of total days = 329; number of stops = 101, number of flights = 228.)

Fixed Effects	**β**	**SE**	***z*-value**	***P***
Intercept	0.68	1.85	0.38	0.71
Air Distance Flown	-1.07×10^{-3}	4.66×10^{-4}	-2.29	0.02
Air Distance Flown^2	5.84×10^{-7}	4.26×10^{-7}	-1.37	0.17
Residual Air Pressure^2	-3.99×10^{-4}	1.26×10^{-4}	-3.16	0.001
Residual Air Pressure	-0.03	0.01	-2.18	0.03
Headwind	0.04	0.06	0.66	0.51
Long-Term Mean Soil Moisture Level	1.23	3.14	0.39	0.70
Maximum Wind	-0.02	0.09	-1.82	0.07
Residual Air Pressure x Headwind	-4.34×10^{-3}	1.83×10^{-3}	-2.38	0.02
Random Effects		**σ**		**St. Dev**
Grid Cell		0.51		0.71
Individual		0.00		0.00
Year		8.68×10^{-14}		2.95×10^{-7}

Causes of Unexpected Stopovers

Of the 99 stops made by godwits, 49 were in expected grid cells and 50 in unexpected grid cells. The six different hypotheses also had significantly different abilities to explain differences between expected and unexpected stopovers (Table 4.5). The best model was again the Global model ($w_i = 0.99$) and it included maximum wind encountered the day a bird stopped, real distance flown and its quadratic term, residual air pressure and its quadratic term from grid cell in which the bird stopped, maximum headwind experienced the day the bird stopped, average soil moisture level encountered the day a bird stopped, and an interaction term between residual air pressure and headwind. The next best model was the Extreme Weather model, with a ΔAIC = 18.4 and $w_i < 0.01$. Only average soil moisture level encountered ($\beta = -0.87$, SE = 0.44, $t = -2.02$ $P < 0.05$) had a significant slope coefficient in the Global Model, although most variables were marginally significant (Table 4.6).

Effects on Arrival Date and Breeding Success

The number of total and unexpected stops made by an individual, as well as the cumulative real distance flown, significantly affected its arrival date at the breeding site, but these had no influence on future breeding success. Using GLMMs, the total number of stops made by an individual has the largest effect on its arrival date (GLMM, $D = 189.3$, $w_i = 0.70$; Number of Stops, $\beta = 1.72$, SE = 0.34, $t = 5.00$, $P < 0.01$), but the number of unexpected stops made (GLMM, ΔAIC = 1.7, $D = 193.3$, $w_i = 0.30$; Number of Unexpected Stops, $\beta = 1.72$, SE = 0.37, $t = 4.69$, $P < 0.01$), and the cumulative real distance flown (GLMM, ΔAIC = 23.4, D = 198.4, $w_i < 0.01$; Accumulated Distance, $\beta = 1.8 \text{ X } 10^{-3}$, SE = $5.83 \text{ x } 10^{-6}$, $t = 3.10$, $P < 0.01$) were also significant predictors.

TABLE 4.5: Model selection for the effects of environmental conditions on the use of unexpected stopover sites during the migration of Hudsonian Godwit, 2010-2012.

Model	**K**	**Deviance**	**AIC**	**ΔAIC**	w_i
Global	8	19.61	41.6	0	0.99
Extreme Weather	4	64.47	78.5	18.4	<0.01
Past Habitat Availability	2	71.44	81.4	19.9	<0.01
Current Habitat Availability	3	79.25	91.3	24.8	<0.01
Approach Conditions	5	121.5	137.5	71.0	<0.01
Random Events	2	139.9	145.9	79.4	<0.01
Accumulation of Poor Conditions	4	139.8	153.8	87.3	<0.01

TABLE 4.6: Model coefficients for factors explaining the use of unexpected stopover sites during the migration of Hudsonian Godwits 2010-2012. All environmental conditions are measured on a daily time scale. (Number of total stops = 101; number of expected stops = 49; number of unexpected stops = 52.)

Fixed Effects	**β**	**SE**	***z*-value**	***P* <**
Intercept	0.32	0.02	1.96	0.05
Air Distance Flown	-9.47×10^{-3}	4.93×10^{-3}	-1.92	0.06
Air Distance Flown^2	-6.06×10^{-6}	3.37×10^{-6}	-1.80	0.07
Residual Air Pressure	0.58	0.30	-1.95	0.06
Residual Air Pressure^2	0.002	0.01	-1.95	0.06
Headwind	0.57	0.38	1.51	0.14
Maximum Wind	1.86	1.14	1.63	0.11
Residual Air Pressure x Headwind	0.09	0.06	1.50	0.13
Average Soil Moisture Level	-0.87	0.44	-2.02	0.05
Random Effects		**σ**		**St. Dev**
Individual		0.64		0.80
Year		0.09		0.30

None of the variables, however, had a significant effect on breeding success (Number of Stops, β = -0.25, SE = 0.45, z = -0.54, P = 0.59; Number of Unexpected Stops, β = -0.07, SE = 0.42, z = -0.17, P = 0.87; Accumulated Distance, β = 4.53 x 10^{-5}, SE = 5.47 x 10^{-4}, z = 0.08, P = 0.93).

Geographic and Temporal Variation in Weather Conditions

The best model in the second stage of the analysis (Table 4.6) indicated that high winds and low air pressures were associated with occurrence of unexpected stopover sites. Headwinds were more than 1 kmh^{-1} stronger on days when birds stopped in unexpected locations than they were on days that they stopped in expected locations (2.81 ± 1.33 vs 1.76 ± 1.51 kmh^{-1}). Air pressure anomalies were more than 3 hPa lower on days of unexpected stops than expected stops (-5.11 ± 6.21 vs. -1.84 ± 0.97 hPa). Wind differed strongly geographically (Figure 4.2). A GLMM with Year as a random effect found that wind varied significantly, with more northerly zones having a higher incidence of headwinds stronger than 2.8 kmh^{-1} (β = 0.14, SE = 0.04, P < 0.01). Wind did not differ temporally, as a GLMM detected only a weak trend for higher incidence of strong headwinds later during the migration period (β = 0.05, SE = 0.05, P < 0.15). Low residual air pressures were more likely to be encountered during the middle of the migration period and the relationship was explained best by a quadratic relationship (β = 0.01, SE = 0.04, t = 3.49, P < 0.05; Figure 4.3**)**. Soil moisture levels were also an important component of both the first and second stage models. Long-term mean soil moisture levels were higher at expected stops (0.57 ± 0.05 mm) than unexpected stops (0.54 ± 0.09mm) and at all stops (0.56 ± 0.01) than on flight days (0.52 ± 0.01; Figure 4.4). Long-term mean soil moisture levels did not vary significantly geographically (Figure 2c; β = -0.003, SE = 0.003, P = 0.45), but did differ temporally, with soil moisture levels rising throughout the migration period (β = 1.75 x 10^{-4}, SE = 2.0 x 10^{-5}, P < 0.01).

DISCUSSION

This is the first study to explore the connection between migration timing, stochastic weather events, and breeding success over multiple years for a group of individual migratory birds tracked daily through their migration. We found that stochastic weather events, especially the occurrence of strong winds and low air pressures, indicating storm fronts, caused migrating godwits to stop unexpectedly during their northward migration from southern Chile to sub-arctic Alaska. Each unexpected stopover delayed an individual's arrival at its breeding site by nearly two days, but did not ultimately affect its breeding success. With projected increases in midcontinental winds, decreases in midcontinental wetlands, and the progressively earlier onset of spring on their breeding grounds, such delays may detrimentally affect reproductive success in the future (Cook et al. 2008, Johnson et al. 2010, Chapter 2). Adaptation to these changes may be difficult given the extreme nature of godwit migration and their reliance upon long, non-stop flight and a small number of regular stopover sites (Chapter 3).

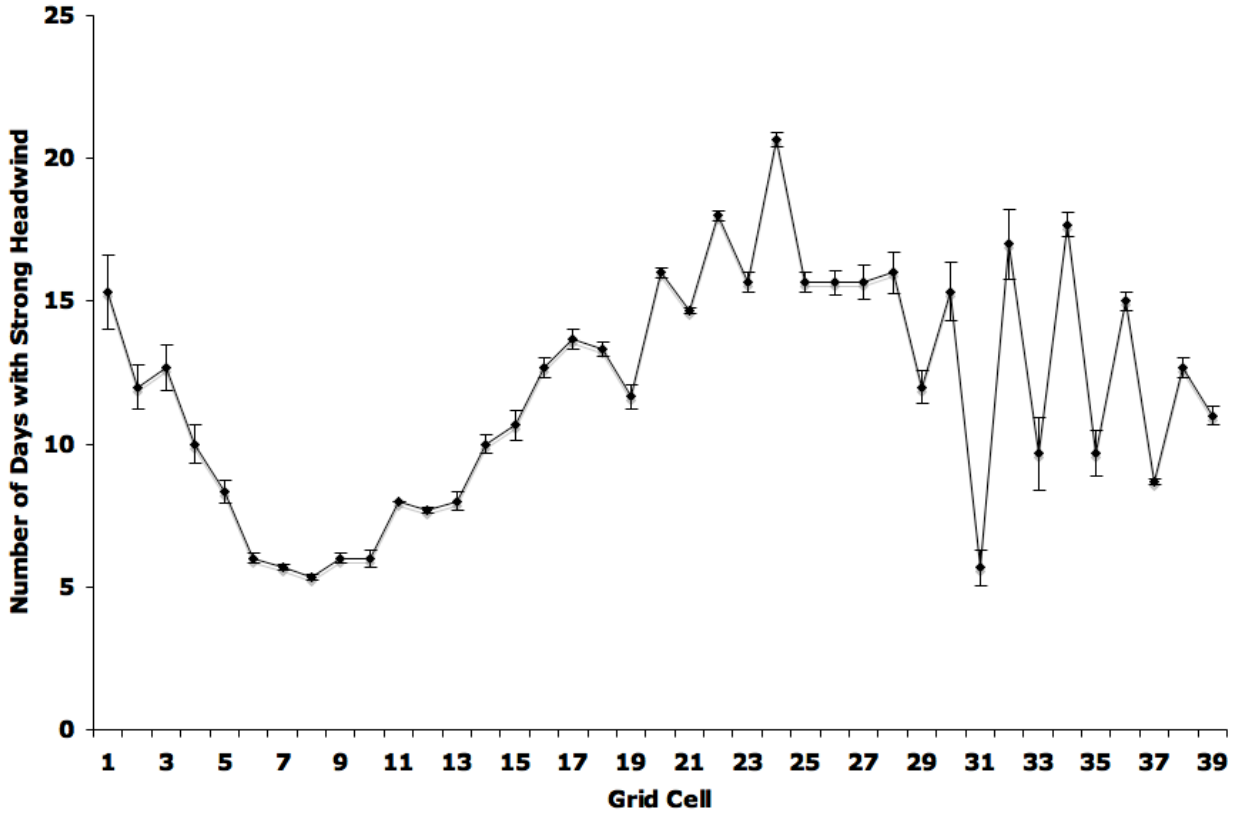

FIGURE 4.2: Geographic variation in the occurrence of strong winds along the migration corridor of Hudsonian Godwits 2010-2012. Days during the 7 Apr-10 May migration period with wind > 2.8 kmh^{-1} — which was identified as the wind speed leading godwits to make unexpected stops during their migration — were tallied for each grid cell along the godwit migration corridor and averaged across years.

Differences Between Flights, Normal Stops, and Unexpected Stops

Individuals that experienced stronger winds (tailwinds), were flying over traditionally drier regions, and had flown less far since last stopping were more likely to keep flying than to stop (Table 4.4). Individuals that experienced stronger headwinds the day of their stop and throughout their flight, as well as lower air pressures, were more likely to stop unexpectedly in drier conditions than to continue on to traditional, wetter stopover sites (Table 4.6). Such a mixture of conditions correlating with the use of stopover sites suggests that decisions based both on weather and physiology govern where and when godwits stop during migration.

All godwits flew nonstop from southern Chile, at least as far as the Pacific coast of Mexico, and most reached the central Great Plains without stopping (Figure 4.1). During their entire flight north over the Pacific, most godwits benefited from sustained tailwinds and began crossing the Gulf of Mexico having flown less far (in air distance) than they would have under windless conditions (Figure 4.5). Crossing the Gulf of Mexico, however, frequently requires flying into sustained headwinds (Figure 4.2) and provides no stopover opportunities. For instance, godwit "XL" encountered significant headwinds during its Gulf crossing in 2010 (Figure 4.6), and required three days to cross the region when it only required one day in both 2011 and 2012. Despite the severe headwinds, XL did not stop, but did begin moving westward toward the Mexican coast. Headwinds are rare the along the Gulf Coast region of the United States during the northward migration period, occurring on fewer than 15% of days (Figure 4.2), but when they do occur, they likely account for those few individuals making stops in this region (Figure 4.1). Headwinds become more common as godwits move north through the midcontinent and the number of godwits stopping slightly south of their primary staging areas increases accordingly. These stops remain rare (Figure 4.1), and are likely sub-optimal, as soil moisture

levels in the region are drier than those found to the north (Figure 4.3).

Kansas, Nebraska, and southern South Dakota provide the core region used by godwits during their northward migration. This likely is the result of a confluence of physiological limits on flight distance (Piersma 2011) and the occurrence, historically, of extensive and reliable wetland habitat (Johnson et al. 2010). Even during the relatively dry study period 2010-2012, during which drought-stricken midcontintenal wetlands were greatly reduced, this region still provided wetter conditions than more arid regions to the south (Figure 4.4), yielding significant wetland habitat (Webb et al. 2010).

After departure from traditional staging areas, godwits track northwest across the Inter-Mountain West, frequently encountering strong headwinds, stalled low pressure systems, low temperatures, and arid soil conditions (Figure 4.2). Strong storms, bringing high winds and sub-zero temperatures moved through the region during the middle of the migration period in all years (Figure 4.2c), but especially 2010 and 2012, forcing some godwits to stop in the region (Figure 4.1). For instance, godwit XL made a one-day stop in eastern Montana in 2011 in the face of just such a storm (Figure 4.3). Following the Inter-Mountain West, godwits arc first west and then north across the open North Pacific (Figure 4.3) before arriving at their breeding site in southcentral Alaska. During this period they also frequently encounter strong headwinds (Figure 4.2a), but as with their crossing of the Gulf of Mexico, are unable to stop. Encountering headwinds over the Pacific is a strong factor delaying arrival at breeding sites and caused godwit XL to spend five days of non-stop flight crossing the region in 2011, leading it to arrive eight days later than in either of the other two years (Figure 4.3).

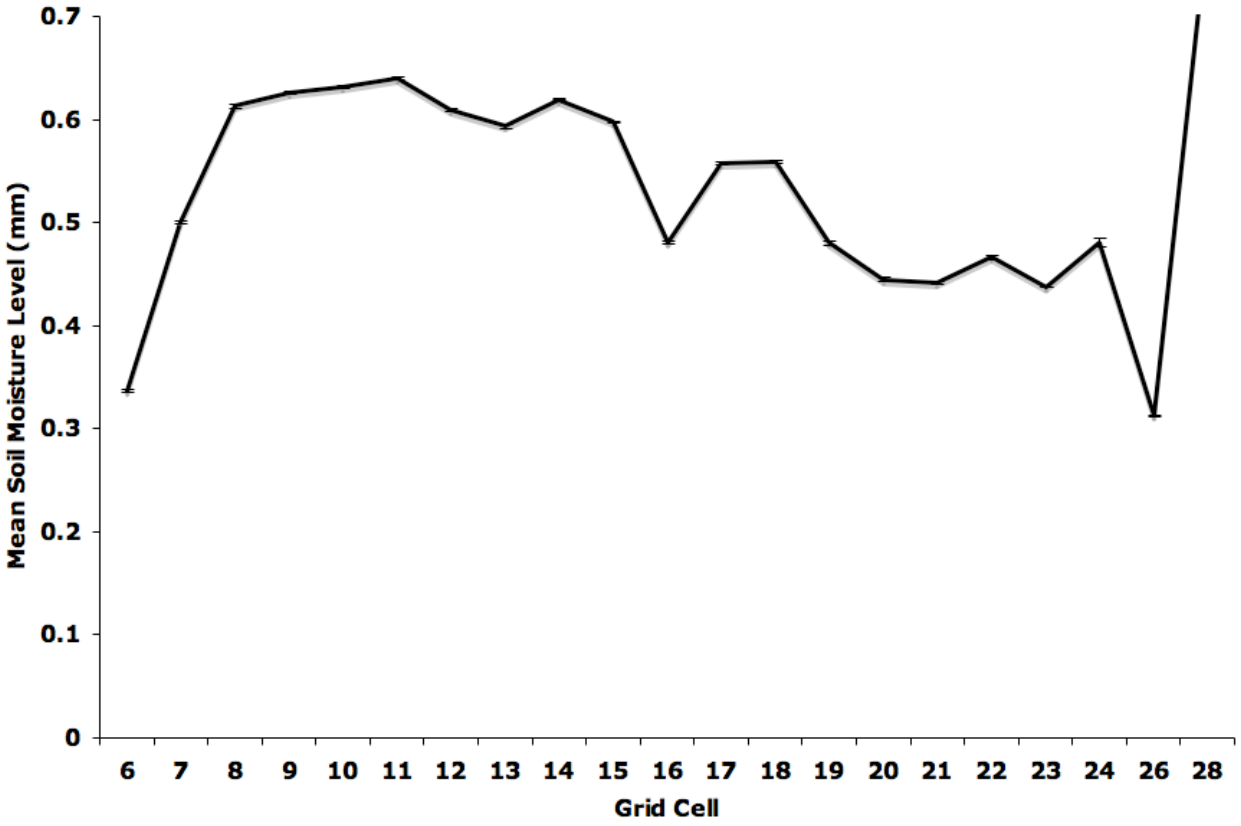

FIGURE 4.3: Geographic variation in long-term (1916-2008) soil moisture levels (mm) along the migration corridor of Hudsonian Godwits 2010-2012. Stopover sites had an average long-term soil moisture level of 0.54 mm, while unexpected stopover sites had an average of 0.57 mm. Soil moisture levels were only available for the continuous United States, corresponding to grid cells 5-28 (see Figure 4.1). Error bars represent standard error, but error is so small that bars are largely not visible.

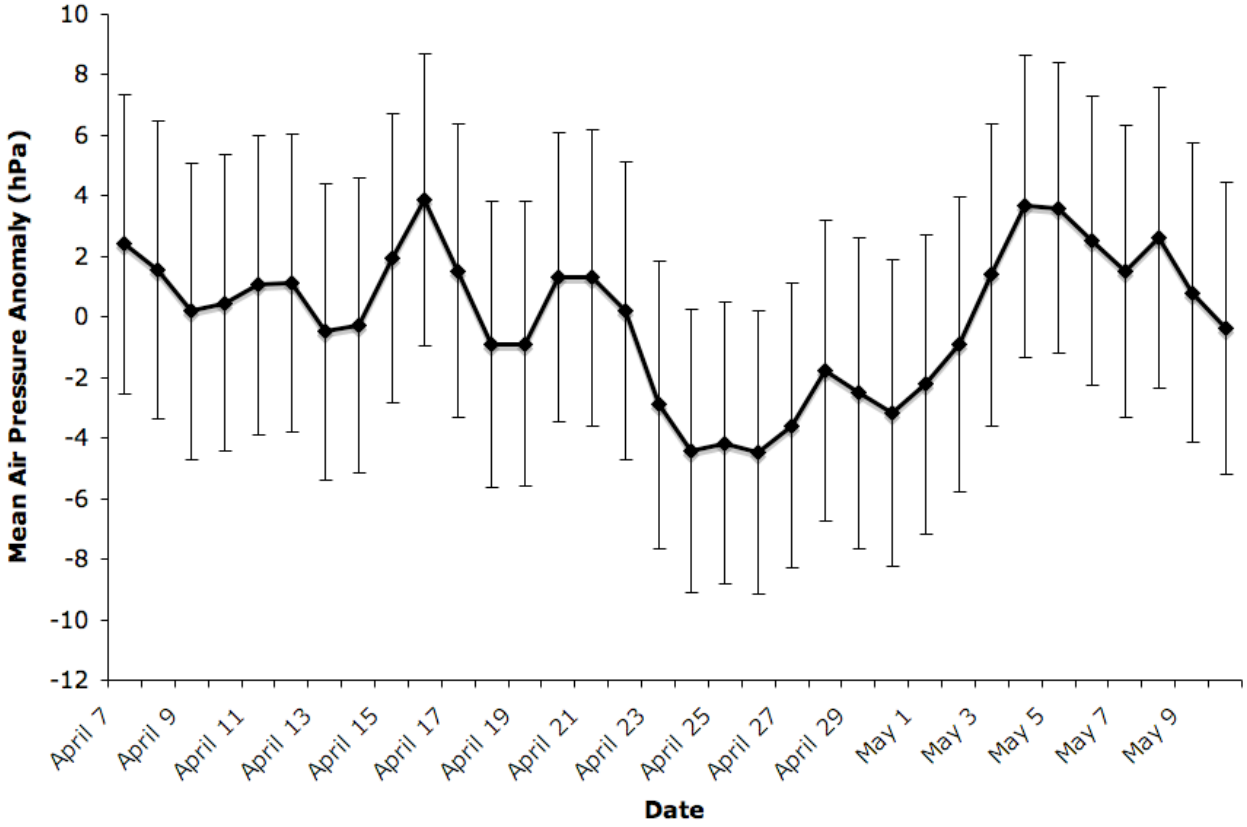

FIGURE 4.4: Temporal variation in the occurrence of mean air pressure anomalies by date across all grid cells 2010-2012. Anomalies were calculated by regressing air pressure against mean grid cell latitude. Anomalies < -5.11 hPa corresponded with Hudsonian Godwits making unexpected stops. Error bars represent standard error.

Effects of Migration on Breeding Success

Although godwits that stopped more frequently and encountered stronger headwinds during their migration were delayed in arriving at breeding sites by nearly two days with each additional unexpected stop, delays did not affect reproductive performance. This likely has to do with two important factors affecting godwits breeding at Beluga River, but which are not common among other godwit populations or migratory birds in general. First, despite climatic changes that have caused the timing of the local peak in invertebrate abundance to shift 14 days earlier, godwits breeding at Beluga River still successfully time their reproductive efforts and, on average, hatch their young eight days prior to the onset of the peak period of invertebrate abundance (Chapter 2). Thus a Beluga-bound godwit would have to stop more than four times before potentially being unable to hatch its young prior to the onset of the peak period of insect abundance. Only two godwits were so delayed across all years. This means that the Beluga River godwit population, unlike other godwit populations, currently has a healthy buffer between their arrival and the optimal timing of laying, incubation, and hatch (Both 2010, Chapter 2). Second, the Beluga River population currently is able to maintain an annual cycle free of carry-over effects, because its annual cycle contains buffer events that are able to ameliorate previously accumulated stresses (Chapter 3). Beluga River godwits may thus be able to push their physiological limits, potentially allowing them to arrive late, transition quickly to breeding readiness, and still properly time their reproductive efforts (Vezina et al. 2012).

It is important to note, however, that in spite of this buffer, unexpected stopovers are sub-optimal. Migrating godwits must alter their physiology while at stopover sites in order to properly refuel for subsequent long migratory flights, a process that can take up to four days (Piersma 2002). Thus, a godwit forced to stop unexpectedly at a poor quality site must make an

important decision: It must either rebuild its digestive tract in order to completely refuel, or it must forgo extensive feeding and wait until the (presumably) poor weather conditions have passed and it can migrate further north to higher quality sites. We found that stopover durations at unexpected sites were less than 1/3 of those at expected sites. Simply put, unexpected stops are made only in extremely poor conditions and appear to provide no benefit to an individual other than allowing it to avoid flying in poor weather conditions. This suggests that other, more time-constrained species, might be unable to make such stops without future repercussions (Gunnarsson et al. 2005, Studds and Marra 2011).

Whether godwits breeding in Beluga River will continue to maintain such a migration and properly time their reproductive efforts in the future is uncertain. This study shows that a migration that proceeds without delays is dependent, in part, on favorable winds, lack of major storms, and good habitat availability. Meeting all three criteria depends on conditions in at least four separate climatic regimes along the migration corridor. Godwits encounter different wind regimes in the South Pacific, Gulf of Mexico, midcontinental U.S., and Inter-Mountain West and North Pacific (Figure 4.2, Figure 4.5). Soil moisture regimes also appear to change at least three times (Figure 4.4) across the midcontinental U.S. The likelihood that each of these regimes changes synchronously over the next century is extremely low (Baker et al. 2004), meaning that godwits will not merely be able to maintain their current *status quo*.

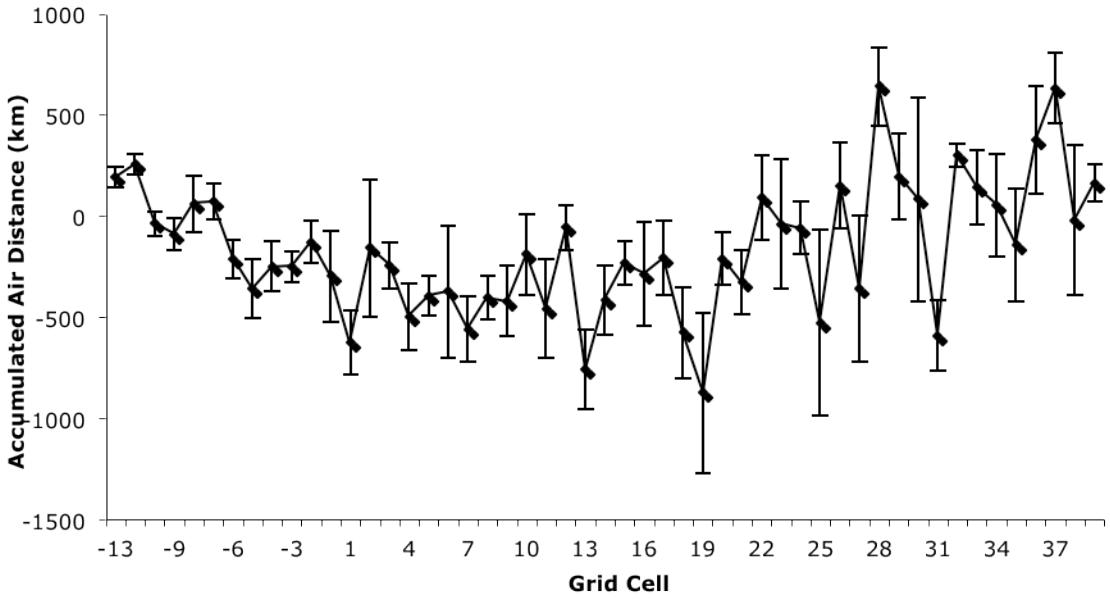

FIGURE 4.5: Geographic variation in accumulated real distances flown by individual Hudsonian Godwits during their northward migrations 2010-2012. Accumulated real distances (km) flown by migrating godwits given wind conditions experienced during their flights were averaged per grid cell. Positive values indicate that an individual had flown further than they would have in still air conditions. A negative value indicates that they received wind assistance and flew less far than they would have in still air conditions. All error bars represent standard error.

Projected changes to the climate and weather encountered by migrating godwits include increased prevalence of ENSO events, which lead to droughts on their non-breeding grounds (Timmermann et al. 1999); increasingly strong winds in midcontinental North America, leading to increases in average wind speeds of up to 3.0 kmh^{-1} (Cook et al. 2008); increasingly severe droughts leading to wetland losses of potentially > 50% in parts of midcontinental North America (Johnson et al. 2010); and unpredictable, yet potentially dramatic, changes to the Aleutian low, which dominates North Pacific winds (Gill et al. 2009). These changes will likely lead to poorer over-wintering conditions, increased headwinds, lower habitat availability and poorer habitat quality, and potentially an increased number of storm tracks along the godwit migration route. Each of these has the potential to disrupt a migration that relies on non-stop flights, frequently into headwinds, of over 10,000 km. For instance, headwinds < 3.0 kmh^{-1} can currently cause godwits to stop unexpectedly. If headwinds double (Cook et al. 2008), all godwits may be forced to make an additional stop south of their core stopover range, in a more arid and drought prone region (Wang et al. 2009), leading to a minimum two-day delay. In contrast to the current flexibility and resilience displayed by Beluga River godwits, other bird populations with extreme migrations have shown that the line between stability and dangerous instability can be very fine (Baker et al. 2004, Chapter 2).

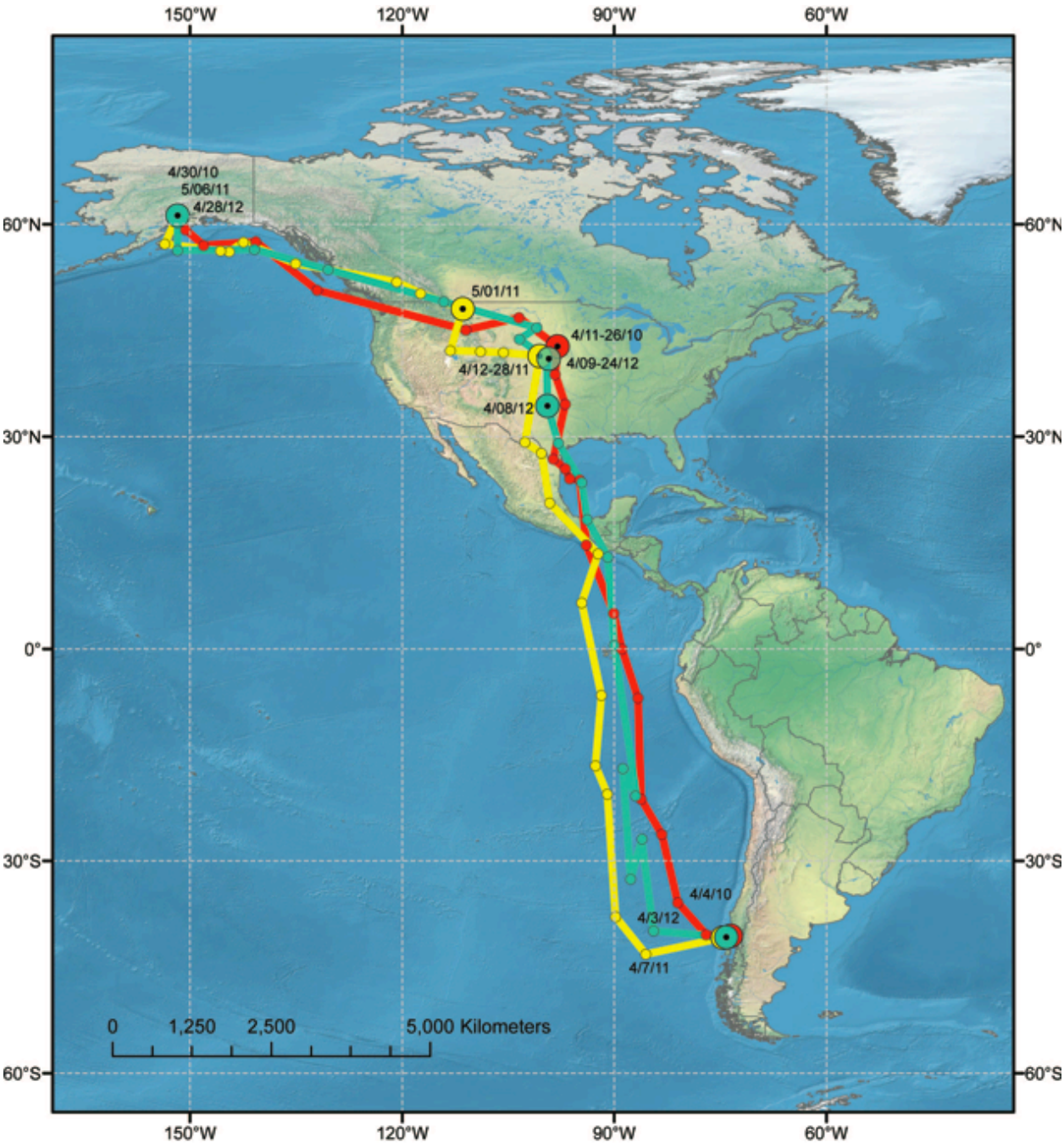

FIGURE 4.6: Repeated migration tracks of female Hudsonian Godwit "XL" 2010-2012, tracked with British Antarctic Survey Mk-14 and Mk-10 geolocation tracking devices. The red line is the 2010 migration track; yellow 2011; and green 2012. Non-breeding, stopover, and breeding sites are denoted with circles with black dots. Departure, stopover, and arrival dates adjoin each site. Daily locations during flights are denoted with open circles.

Responding to Future Changes, Both Stochastic and Predictable

Key to any population's ability to respond to stochastic change simultaneous with changes in mean conditions is the amount of flexibility existing in its annual cycle. Populations with tightly overlapping and contingent stages of the annual cycle have less capacity to withstand changes that disrupt or prolong any one stage (Wingfield 2008). Extreme weather events, which are frequently unpredictable, are particularly difficult in this regard for migratory populations, which tend to have little flexibility in their annual cycles (Wingfield 2008, Canale and Henry 2010). Godwits show that despite preparations that allow them to make tremendously long, non-stop flights, extreme weather events can cause them to make unexpected stops and these stops have measurable, if currently benign, repercussions. Any climatic changes that increase the intensity and frequency of storms during these non-stop flights are likely to have particularly dramatic effects (Villarini and Vecchi 2012). However, so long as such events remain both rare and unpredictable, their effects will likely remain trivial in comparison to the projected changes in mean conditions along their migration corridor (Smith 2011). On the other hand, continued changes in mean conditions eventually could destabilize the godwit annual cycle by inducing the accumulation of carry-over effects and mistimed reproductive efforts, so that stochastic events will pose a more significant challenge to the population's health (Foley 1994). Other godwit populations have been shown to lack this flexibility already (Chapter 2), and currently may be vulnerable to decline as the direct result of stochastic events (Wingfield 2003, Chapter 2).

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CHAPTER 5

PREDICTING THE CONSEQUENCES OF CLIMATE CHANGE FOR LONG-DISTANCE MIGRATORY BIRDS: A FULL ANNUAL CYCLE APPROACH

Nathan R. Senner

ABSTRACT

Predicting how global climate change could affect a given species or population is a fundamental question now facing ecologists and evolutionary biologists. Much research has focused on climate change, but it has rarely facilitated assessment of how a specific species or population will be affected and how it might respond to future climate-related changes. Employing an organism-environment approach to the entire annual cycle, I use the lens of the Hudsonian Godwit, *Limosa haemastica*, to explore how migratory birds may be affected by climate change during the coming century. One Hudsonian Godwit breeding population is mismatched with the local resource phenology necessary for it to successfully breed, while another breeding population is not. This difference results from underlying variation in the amount of flexibility existing in their annual cycles and leads them to be differentially vulnerable to other climate-change related changes occurring throughout their annual cycles. Such intra-specific variation suggests that the amount of annual-cycle flexibility available to a population, and thus the danger that transition periods and mature phases of their annual cycle will be forced to overlap, is critical to the breeding success and survival of the population under future climate change scenarios. Understanding the flexibility existing within a species' annual cycle, identifying those transition points likely to be affected by climate change, and assessing the degree to which

separate stages of the annual cycle may overlap, together yield a basic framework for predicting how species will be affected by future climatic change. This framework should enable a robust assessment of those species currently at greatest risk.

INTRODUCTION

What predicts the consequences of climate change for a given species? This has become a fundamental question given the rapid and frequently asynchronous climatic changes currently affecting much of the globe (IPCC 2007), but its answers are neither easy nor straightforward. A rapidly growing body of literature evaluates the effects of climate change on organisms across trophic levels and ecosystems, and a recent Web of Science search for the terms "birds" and "climate change" returned 2,177 articles, 246 of which were published during the first eight months of 2012 alone. Included in these articles is a dizzying array of predictions for how specific taxonomic groups will fare in the future (Philippart et al. 2011, Sydeman et al. 2012, Wolkovich et al. 2012). Many unknowns remain about the effects of climate change on organisms and climate change's future trajectory, and thus, despite this substantial body of research, a common framework that can be used to identify how climate change will affect specific species and populations has yet to be developed (Wingfield et al. 2011).

This lack of a common framework is understandable. Some species have exhibited phenotypically plastic responses to climatic change, while others have not, and still others appear to be adapting genetically instead of phenotypically (Donnelly et al. 2012). Some species are declining precipitously, while others remain stable or are even expanding (Donnelly et al. 2012). Recent theoretical advances, however, do suggest an overall framework for evaluating a species' future status under climate change: Events taking place throughout a species' annual cycle can

affect its breeding success and survival (Harrison et al. 2011) and this linkage of events across the annual cycle makes it imperative to consider the effects incurred from selection pressures occurring throughout the year (Ådahl et al. 2006, Buehler and Piersma 2008, Both 2010, Wilson et al. 2011). Achieving such an understanding for a given species, in turn, requires knowledge of the interactions between an organism and its environment at each stage of its annual cycle (Wingfield et al. 2011). Coupled with the fact that climate change is a global phenomenon, having varying local- and regional-scale regimes, any evaluation of the effects of climate change on a species, especially a migratory species, must consider that species' entire annual cycle.

Using the entire annual cycle approach of Ådahl et al. (2006) and the organism-environment approach of Wingfield et al. (2011), I explore here how climate change can affect a species or population at each stage of its annual cycle using the lens of a long-distance migratory bird, the Hudsonian Godwit, *Limosa haemastica*, to generate a set of testable predications hopefully applicable to other taxa. My intents are (1) to simplify the process of addressing potential effects of climate change on a given species and, (2) to focus on the importance of studying migratory populations over their entire annual cycle.

FOCAL SPECIES

The Hudsonian Godwit (hereafter, 'godwit') is a long-distance migratory shorebird that breeds in three disjunct populations spread across the Arctic and sub-Arctic of Canada and Alaska — the Hudson Bay lowlands of northern Ontario, Manitoba, and Nunavut; the low-Arctic of the Northwest Territories and northeastern Alaska; and sub-arctic southcentral and western Alaska. These three populations are connected, respectively, to three separate non-breeding populations in Argentina and Chile — Tierra del Fuego and the southern coast of Patagonian Argentina; the

Buenos Aires province of northern Argentina; and Isla Chiloé and the adjacent Chilean mainland (Walker et al. 2011).

During the non-breeding season, godwits prefer large intertidal bays with soft-sediment mud that enables them to probe deeply for benthic prey items, such as the mussel, *Darina solenoides* (Bala et al. 1998, Senner and Coddington 2011). Fueling for molt and northward migration likely take up much of a godwit's time and energy during this period. Godwits complete both their prebasic and prealternate molts while at non-breeding sites (Walker et al. 2011), which in other *Limosa* species is a time-consuming process (Conklin and Battley 2012). Departure for northward migration is largely synchronous within a breeding population, typically spanning little more than one week (Chapter 3).

Godwit migration is among the longest recorded for any bird, spanning nearly 16,000 km twice each year (Chapter 3). Most of this distance is covered in a series of multi-day, non-stop flights covering up to 10,000 km and 7 days — the second-longest recorded flights among migratory birds (Gill et al. 2009, Chapters 3,4). In between these non-stop flights, each godwit population stops at a suite of traditional staging regions (Figure 5.1) where it can spend up to six weeks recovering and refueling for future flights (Warnock 2010, Chapter 3). In total, northward migration spans slightly less than one month and southward migration often more than two months (Walker et al. 2011, Chapter 3). Northward migration phenology (as well as breeding phenology), however, is offset by approximately one month between the three populations: Alaskan godwits migrate northward beginning in early April and arrive at breeding sites by the first week of May, while Hudson Bay and northwest Canadian godwits leave non-breeding sites in early May and arrive at breeding sites in late May and early June (Walker et al. 2011, Chapters 1,3).

The godwit breeding season is brief. Adults are present at breeding sites for no more than 10 weeks, and fewer in some years (Chapter 2). Pairs are formed nearly immediately after arrival at breeding sites and the first eggs are laid within a week of return. Four-egg clutches are complete for most pairs within 10 days and hatch commences 22-23 days later (Walker et al. 2011). Although godwits never double-brood, nest predation can be high in some years, frequently leading pairs depredated early in the season to lay replacement clutches. Chicks leave the nest almost immediately upon hatch and spend the pre-fledging period traversing the landscape feeding on insects and other small invertebrates (Chapter 2).

Godwit chick growth is rapid (Chapter 2), as is typical among Arctic-breeding shorebirds and is much faster than temperate-breeding species in the same genus and family (Beintema and Visser 1989, Schekkerman et al. 2003). Chicks fledge at about 28 days and adults move from breeding to staging sites at around this time (Chapters 2,3). Juveniles begin preparing for migration as much as a month later (Walker et al. 2012).

Annual survival rates for adults are high, usually exceeding 80% (Chapter 3, Senner unpubl. data). Godwits, however, don't breed until ~3 years of age and their survival rate (and whereabouts) up to that point are unknown (Walker et al. 2011). Returning to a natal site as a breeder is rare (about 2% of individuals; Senner unpubl. data). Inter-seasonal variation in survival rates is currently unknown. At the very least, mortality rates are low during the breeding season (Senner unpubl. data).

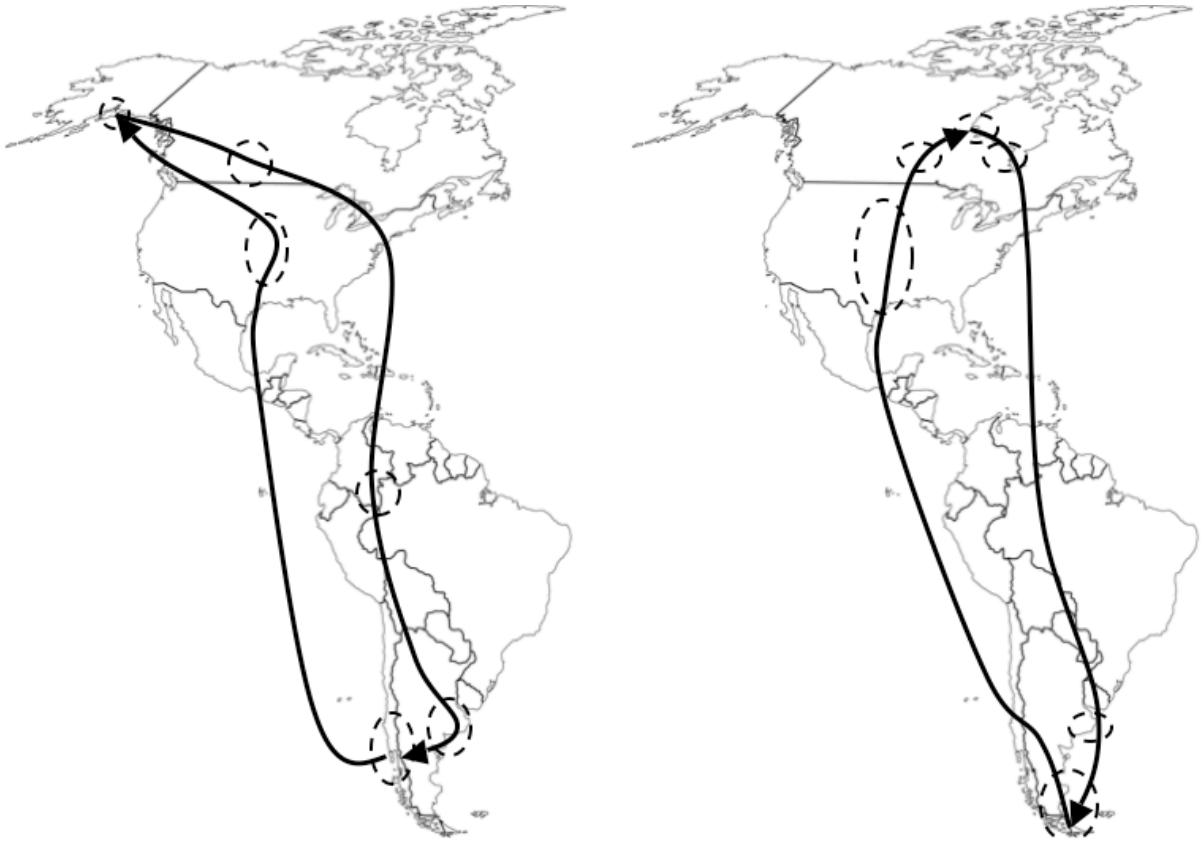

FIGURE 5.1: Migration routes and stopover, breeding, and wintering sites of Hudsonian Godwits breeding at (a) Beluga River, Alaska, United States and (b) Churchill, Manitoba, Canada. Data was originally collected from British Antarctic Survey Mk-14 and Mk-10 geolocation tracking devices and published in Walker et al. 2011 and Chapter 3. In (a), sites (clockwise from south to north) are Isla Chiloé, Chile; central Great Plains of Kansas and Nebraska, United States; upper Cook Inlet, Alaska, United States; central Saskatchewan, Canada; Guainía Department, Colómbia; and Buenos Aires Province, Argentina. In (b), sites are Tierra del Fuego; midcontinental United States; central Manitoba, Canada; Hudson Bay, Manitoba, Canada; James Bay, Ontario, Canada; and Buenos Aires Province, Argentina.

CLIMATE CHANGE AND THE ANNUAL CYCLE OF MIGRATORY BIRDS

The annual cycle of a migratory bird can be subdivided into five or six stages, depending on a species' molt strategy — non-breeding season, prealternate molt, vernal migration, breeding season, prebasic molt, and autumn migration (Figure 5.2; Wingfield 2008). These stages overlap to varying degrees and can further be divided into sub-stages, such that each of the separate components comprising an individual's annual cycle can be linked to, and controlled by, both environmental and endogenous conditions. With respect to the godwit annual cycle, I condense these six annual cycle stages into four — the non-breeding season (which includes both prebasic and prealternate molt), northbound migration, breeding season, and southbound migration.

Each stage of the avian annual cycle can be affected by climate change, either separately or in concert with other stages, through linkages known as carry-over effects (Carey 2009). For instance, northward migration in European songbirds can be delayed by drought conditions on their non-breeding grounds in the African Sahel, which in turn affects their ability to time their breeding efforts in the north temperate zone of Europe with the progressively earlier peak in food resources occurring there (Both 2010, Robson and Barriocanal 2011). Conversely, increased incidence of extreme weather on the breeding grounds may reduce breeding success, but may not affect subsequent stages of the annual cycle or long-term adult survival (Wingfield et al. 2011). Therefore, some consequences of climate change may have more pervasive effects on the avian annual cycle (i.e., phenological changes in resource availability), while others may have more limited affects (i.e., incidence of extreme weather, altered habitat availability).

In general, the potential effects of climate change on each stage of the annual cycle can be broken down into six types: 1) Changes in phenology can alter the timing of important events, such as the appearance of food resources, and can disrupt the synchrony that has developed

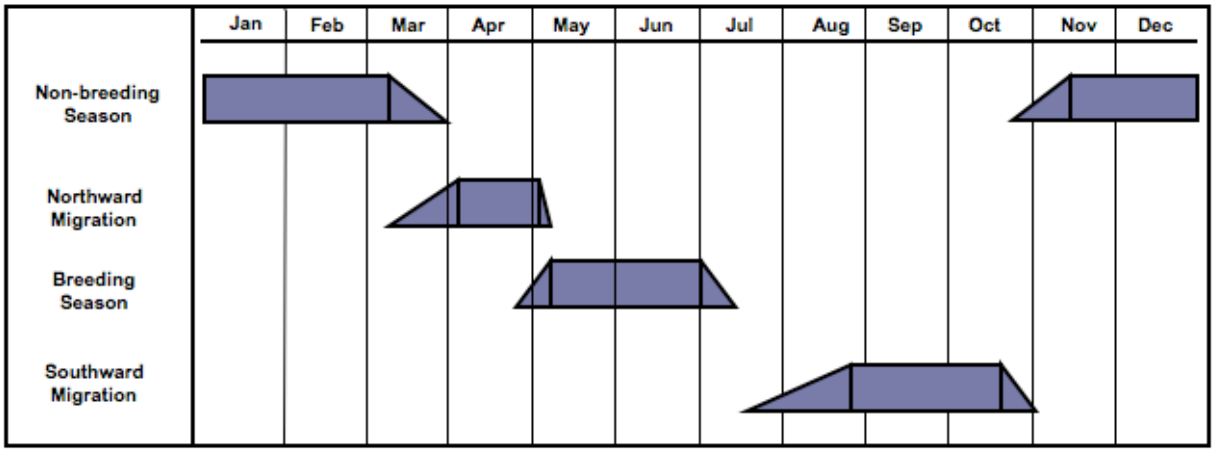

FIGURE 5.2: Organization of the annual cycle and life-history stages of Hudsonian Godwits breeding in southcentral Alaska. (Adapted from Figure 4, Wingfield 2008.) Left-sloping triangles denote the initiation phase of a stage, the rectangle the mature phase, and the right sloping triangle the termination phase. Initiation and termination phases of different stages can overlap and climate change can cause greater overlap during these periods or can delay the termination of one and the subsequent onset of another. Alternatively, it can also prolong or shorten the mature phase of each stage as well. Studies of climate change must take into account the degree to which the overlap of these periods is possible and what cues are used to initiate and terminate each stage

between a species and its primary prey (Durant et al. 2007). 2) Changes in the distribution of a species can bring new species into contact with one another, alter competitive interactions, affect predator-prey relationships, and potentially reduce a species' ability to compete successfully for resources (Harris et al. 2012). 3) Changes in disease prevalence can greatly increase the incidence and impact of a disease in a species, thereby reducing survival (Zamora-Vilchis et al. 2012). 4) Changes in prey behavior can alter food availability and affect both breeding success and survival (Kokubun et al. 2010). 5) Changes in the frequency and intensity of extreme weather events can disrupt migrations and breeding seasons and reduce breeding success and survival (Canale and Henry 2010). 6) Changes in habitat availability — whether through drought, sea-level rise, or the migration of habitat types — can lead to range shifts and density-dependent consequences (Buermann et al. 2011).

CLIMATE CHANGE AND THE ANNUAL CYCLE OF HUDSONIAN GODWITS

Using what is known about the annual cycles of godwits and other long-distance migratory shorebird species, this section explores how the six types of climate-related changes will affect each of the four stages of the godwit annual cycle.

Non-breeding Season

Although shorebirds are a natural reservoir for diseases such as avian influenza, the prevalence of such diseases in godwits and other shorebirds that breed in the Arctic and strongly rely on temperate and sub-Antarctic marine habitats during the non-breeding season is thought to be low (Mendes et al. 2005). Tests of wintering Red Knots, *Calidris canutus rufa*, for avian influenza and other diseases at non-breeding sites that they share with godwits in southern Argentina all returned negative (D'Amico et al. 2007) and, in general, disease prevalence is low among coastal

shorebirds outside of periods spent in the tropics (Mendes et al. 2005). Thus, although certain viral and bacterial diseases are increasing globally (Garamszegi 2010), disease risk to godwits during the non-breeding season appears to be low.

The stressors most likely to affect godwits during the non-breeding season are factors that influence their ability to obtain adequate food supplies to (1) fuel recovery from their southward migration, (2) complete two separate molts, and (3) prepare for northward migration. Godwits currently appear to have little trouble completing these activities. Studies with Bar-tailed Godwits, *Limosa lapponica baueri*, have shown that even individuals arriving late to their non-breeding grounds are able to depart on time and survive through the year (Conklin and Battley 2012). Hudsonian Godwits currently appear to enjoy a similar relative "freedom" from stress during the non-breeding season. Although departure dates vary for individuals by as much as eight days between years, departure date from non-breeding sites does not effect the number of stops made during northward migration nor subsequent breeding success in the Alaskan breeding population (Chapter 3,4). Only relatively small changes may need to occur, however, to alter this situation. Black-tailed Godwits, *Limosa limosa islandica*, in Western Europe occupying low-quality estuaries during the non-breeding season exhibit carry-over effects that result in their late arrival at breeding sites, occupation of relatively low-quality breeding territories, and, ultimately, low reproductive success (Gill et al. 2001, Gunnarsson et al. 2005). Such carry-over effects may not simply result from the occupation of low-quality habitats, but from the further degradation through anthropogenic forces of what already were naturally lower-quality sites (Chapter 3).

Because godwits spend the non-breeding season at temperate and sub-Antarctic latitudes, a warming climate will initially help to ameliorate self-maintenance costs (Piersma 2002). However, models of future climatic change in the Southern Hemisphere project increases in the

frequency and severity of El Niño events, which lead to drought conditions in the region (Timmermann et al. 1999). Increased heat stress can cause shifts in the availability of intertidal benthic invertebrates, such as *Darina* mussels or Polycheate worms, by causing invertebrates to move lower in the benthos or incurring unusually dramatic population fluctuations (Silva et al. 2006, Broitman et al. 2009). Thus, what is generally a highly stable food supply (Ribeiro et al. 2004, Lizarrarde and Pittaluga 2011) can be significantly affected by climatic change, to the point that godwits may incur stress during the non-breeding season.

Sea level rise is another variable with the potential to alter conditions currently experienced by godwits during the non-breeding season. Most model predictions suggest that southern South America will experience only a moderate rise in sea level by the end of the 21st century (Yin et al. 2010, Slangen et al. 2012). However, given the relatively small size of many of the estuaries used by godwits, especially on Isla Chiloé, Chile, even a moderate rise in sea level may be enough to inundate significant portions of the intertidal zone and cause a reduction in godwit foraging habitat (e.g., Galbraith et al. 2002).

Northward Migration

Disease risk is likely highest for godwits during migration. During this period godwits are physically taxed and, when recovering from long flights, less able to mount immune responses (Buehler et al. 2010). Moreover, they are coming into contact with a diverse array of other species that may potentially carry novel disease strains (Lawson et al. 2011) and they are potentially foraging in large, dense flocks that can aid in disease transmission (Maxted et al. 2012). Given this combination of factors and the increased prevalence of many diseases as a result of climate change, it may be a question of when, and not if, a disease outbreak will occur among godwits during migration. How an outbreak may affect godwits at the population level is

hard to predict, as little is known about their specific immune capabilities and shorebird species can vary widely in their susceptibility to diseases (Maxted et al. 2012). Nonetheless, a forecast of potential challenges facing godwits as a result of climate change must include the possibility of a severe disease outbreak.

Altered phenology and increased incidence of extreme weather also have a high potential to affect godwits during migration and, in fact, are already doing so to a significant extent. Although all three godwit breeding populations use the same migratory corridor within central North America — roughly 15 degrees of longitude in width, extending from central Missouri to western Kansas — they do so at slightly different times. This gap in passage dates, with Alaskan godwits passing through the corridor in April and the other two populations in May, exposes the Alaskan population only to warming climatic regimes on their way north, whereas the other two populations encounter conflicting regimes (Chapter 1). For those godwits migrating in May, this means that in the southern portion of the migration corridor they are encountering warming springs, but that in the northern portion of the migration corridor they are experiencing cooling springs. These asynchronous regimes extend north to their breeding grounds and stand in contrast to dramatically warming early summers in the region (Gagnon and Gough 2005a). The result has been that godwits breeding in Churchill, Manitoba, have retarded their arrival on their breeding grounds by more than 10 days in the past four decades, in contrast to godwits breeding at Beluga River, Alaska, which have accelerated their arrival by nearly 9 days during the same time period (Chapter 1).

The exact mechanism by which the migration of Hudson Bay godwits is slowed is not known: Wintry conditions on the breeding grounds could be the sole factor, but the delay of greening and invertebrate emergence at stopover sites, meaning that godwits must spend longer

periods at more southerly stopover sites or refueling at more northerly sites, could also contribute. In either case, the climate and weather conditions that affect the Hudson Bay population during its migration are all changing in ways that will make it difficult for them to speed up their migration, even if cooling spring climate regimes in northcentral North America reverse themselves. Winds and precipitation in Tierra del Fuego during the departure period are declining and projected to decline even further, lessening the number of days on which godwits have tail winds to aid the initiation of their northward migration (Menendez et al. 1999, Vera et al. 2006). Likewise, winds in the central United States during the passage period are increasing and projected to increase even further, creating stronger cross- and headwinds for migrating godwits (Cook et al. 2008).

Asynchronous warming regimes could affect all of the populations in the near future, especially as regional climates begin to diverge more considerably (IPCC 2007). Asynchronous regimes need not be in conflict with each other — with some warming and others cooling — for godwits to be detrimentally affected. If consecutive stopover sites are warming at disparate rates, the ability of godwits to arrive at the appropriate time to make use of resource peaks may be compromised (Bauer et al. 2008). Given the limited number of stops that godwits make en route to their breeding sites (Chapter 3), and because these few stops are connected by multi-day, non-stop flights that stress their physiological capabilities (Piersma 2011), limiting their ability to adequately refuel at some sites could have severe consequences (Baker et al. 2004). Other super long-distance migrants that have suffered similarly compromised staging areas have experienced dramatic population declines, owing to reductions in breeding success and adult survival (Morrison et al. 2004, Yang et al. 2011)

Stochastic weather events are currently the most common factor causing godwits to make

unexpected stops during their northward migration (Chapter 4). All unexpected stops appear to be extra stops, because all individuals visit traditional stopover sites whether or not they have stopped elsewhere en route. These extra stops delay an individual's arrival on the breeding grounds by approximately two days per stop (Chapter 4). Such delays currently do not reduce the breeding success of Alaskan breeding godwits (Chapter 3, Chapter 4), but likely do for the Hudson Bay population (Chapter 2). Future increases in the incidence of extreme weather events (Bukovsky and Karoly 2011) may change this scenario for Alaskan godwits and certainly will exacerbate the already difficult situation facing Hudson Bay godwits. Truly extreme weather events, such as tropical storms occurring during trans-oceanic flights, also have the ability to cause mass mortality events and not merely migratory delays (Newton 2006).

Changing species distributions play a difficult-to-quantify role during this period. Identification of direct competition between godwits and other shorebird species for food resources at stopover sites is lacking and climate change is unlikely to alter shorebird distributions in such a way as to change this scenario (Andrei et al. 2006, 2009). Changes in predator distribution and migration phenology could, however, have a significant impact on godwit migration (Lank et al. 2003). Peregrine Falcon populations have increased steadily over the past three decades and have now recovered to a level at which they have begun to alter shorebird migration timing and strategy (Ydenberg et al. 2007). As climate change differentially alters the migration timing of shorebirds and their predators, timing shifts that cause a greater overlap between godwits and their avian predators could have important consequences for all three godwit populations during their northward migration.

The final factor potentially affecting godwits during migration is habitat availability. Recent years have seen an increase in the number and severity of droughts occurring in

midcontinental North America (Bukovsky and Karoly 2011). Because much of this region is naturally arid, godwits and other migrant shorebirds have evolved to rely on ephemeral wetlands as stopover sites. Any significant reduction in the amount of available wetland habitat could significantly alter and impair godwit migration (Skagen et al. 2008).

Breeding Season

The potential for disease outbreaks among godwits is likely lower during the breeding season than during migration, but cannot be discounted. As in migration, godwits are coming into contact with novel disease strains, particularly from Eurasia via trans-hemispheric migrants such as Northern Pintails, *Anas acuta* (Pearce et al. 2011). Avian influenza exchange rate among waterfowl and shorebirds in the region has been low (Pearce et al. 2012), but has happened and is thus possible (Pearce et al. 2010). Inter-continental disease strain transmission rate is higher closer to the border between continents (Ramey et al. 2010), thus making godwits breeding in western Alaska potentially more susceptible to disease outbreaks than other godwit populations during this time period.

Changing phenological regimes are currently the single biggest challenge related to climate change facing godwits in any season. A phenological mismatch between breeding efforts and local resource phenology is already affecting the reproductive success of godwits breeding at Churchill, Manitoba (Chapter 2). A similar mismatch could also be affecting godwits breeding in northwest Canada given the spring climate change regimes along their migration route, but this has not yet been studied. The Alaska breeding population currently is not experiencing a mismatch and may be able to continue to adapt to the climate change regime occurring in that region (Chapter 1).

The phenological mismatch affecting godwits breeding in Churchill has averaged 8 days

each breeding season from 2009-2011 and has caused chicks to be raised in a period with 7-37% fewer insects and a 50% higher likelihood of experiencing starvation-inducing conditions (Chapter 2). This mismatch is the result of conflicting warming regimes along their migration route and on their breeding grounds and godwits appear to have little ability to reconcile these conflicting regimes. Wintry conditions now persist later into May on their breeding grounds than previously — precluding an earlier arrival — and stand in contrast to the rapid early summer warming that has caused local resource phenology to begin to shift earlier (Chapter 2). An acceleration of projected warming in the Hudson Bay lowlands during the next century will only exacerbate this situation (Gagnon and Gough 2005b).

The increasing loss of permafrost in the Arctic, combined with the northward migration of woody vegetation, mean that godwits also may soon face significant alterations to their breeding habitats (McGuire et al. 2006, Schuur et al. 2007, Virkkala et al. 2008). This may be of particular concern to godwits breeding in the Northwest Territories, whose breeding grounds already reach to the edge of the Arctic Ocean (Senner 2010), but could also affect other populations as the loss of permafrost and increased snow melt allow the Arctic water table to drop below ground and desiccate Arctic wetlands (Woo et al. 2006, Abnizova and Young 2010). Wetlands are particularly important to breeding godwits, as they provide the major foraging habitat for pre-fledging chicks (Pearce-Higgins 2010, Senner unpubl. data). When combined with the already occurring phenological mismatch, wetland loss is a potentially serious threat to godwit breeding success.

Species distributions during the breeding season may change dramatically as a result of climate change (Barbet-Massin et al. 2012), however it is unclear how changes in avian species distributions might directly affect godwits. Changes in predator distributions, especially those of

their main nest predators — such as Arctic, *Alopex lagopus*, and Red Foxes, *Vulpes vulpes* — could have a significant effect on godwit breeding success. Already predation is resulting in low nest success in Churchill (Chapter 2) and future changes to sea ice persistence and lemming cycles could force foxes onto land and into greater reliance of shorebird eggs (Ims and Fuglei 2005). Further reduction in nest success at Churchill could prove nearly as detrimental as an exacerbation of their current phenological mismatch.

Southward Migration

Southward migration receives less attention than northward migration in the climate-change literature, as it is not governed by the need to arrive successfully on the breeding grounds and initiate the breeding process (Van Buskirk 2012). However changes to their southward migration may have a large effect on the future stability of godwit populations. Most dramatically, an increased incidence and strength of North Atlantic hurricanes during the next half-century could present a significant challenge to migrating godwits during their non-stop flight from Canadian staging areas to stopover sites in the Colombian Amazon and northern Argentina (Villarini and Vecchi 2012). Already, tracking studies of southward shorebird migration in the Atlantic have highlighted the frequency with which trans-oceanic flights are disrupted by these storms (F. Smith, pers. comm.). Further increases in storm frequency could lead to increased usage of intermediate and rarely used stopover sites on Caribbean islands (Chapter 3), currently a region of intense hunting pressure (Ottema and Spaans 2008, Watts and Truit 2011). Some storms may also lead directly to mass mortality events (Newton 2006).

A second major concern during this period is the drying of mid-continental wetlands in North America. Fall staging areas in central Saskatchewan act as buffer event sites for Alaskan godwits, allowing them to alleviate accumulated stress from their northward migration and

breeding season (Chapter 3). Twenty-first century climate projections for the northern Prairie Pothole Region suggest significant wetland drying and a reduction in the number of changes in wetland cover cycles, meaning that wetlands will either dry completely and disappear or become stuck in an unproductive vegetative stage (Johnson et al. 2010). Altering the function of wetlands in central Saskatchewan for godwits could have negative downstream consequences, especially if coupled with more difficult trans-oceanic flights.

The final potential stressor for godwits during their southward migration is disease. During their southward migration, Alaskan godwits stopover in the heart of the Amazon Basin for an average of nine days while en route to non-breeding sites in southern Chile (Chapter 3). Studies have shown that disease incidence in shorebirds is highest while in tropical and inland wetlands (Mendes et al. 2005) and also while recovering protein after long migratory flights (Buehler et al. 2010). Southward migration may thus be the period when this population is most susceptible to disease. Hudson Bay godwits do not regularly stopover in the region (Figure 5.1), suggesting that disease may be less of an issue for them during this period.

Changes in prey availability, resource phenology, and species distributions are all less likely to affect godwits during this period than in other parts of the year. Each could play a role in some circumstances — increasing occurrence of droughts in the Amazon Basin, for instance (Marengo et al. 2012) — but none pose an imminent or clear threat.

THE WAY FORWARD

All of these many climate-change related factors could potentially act in concert to completely alter the godwit annual cycle. It is far more likely, however, that some will present more of a challenge than expected and others will not come to pass at all. Looking at the godwit annual

cycle and using the organism-environment framework, three observations could inform the process of considering climate-related scenarios for other species and populations:

1) Some populations and species have more flexibility in their annual cycles than previously thought (Donnelly et al. 2012, Chapter 1). Thus, it should not be assumed *a priori* that any species or population will be negatively impacted by any single challenge presented by climate change. However, the fact that one godwit population already is experiencing a significant reduction in its breeding success confirms that some negative impacts are already underway (Chapter 2). Another godwit population has been able to adapt to a 14-day shift in resource phenology on their breeding grounds through a corresponding acceleration of their arrival time (Chapter 1), meaning that the effects of climate change can dramatically vary even within a single species.

Assessing the amount of underlying flexibility occurring within a population's annual cycle is difficult. The godwit story illustrates that a narrow dividing line separates situations in which flexibility is sufficient to accommodate climatic changes and those in which flexibility is insufficient. Part of the difficulty in assessing flexibility is that can take a number of forms and understanding which scale is most relevant to a particular situation is not always straightforward. At the smallest scale, flexibility can be related to a species' organization of its annual cycle. For instance, a species whose annual cycle includes a sequence of non-overlapping stages likely has less flexibility than do species with overlapping stages. In the former case, each stage must be completed in succession and is governed by its own distinct set of physiological, morphological, and behavioral changes. These, in turn, are governed by hormonal changes, each of which also must complete its own cycle of development, expression, and termination (Wingfield 2008). A second type of flexibility involves cues used by a species to initiate each stage of its annual cycle

(Wingfield 2005). Some cues may be simple, such as temperature change, while others may be complex or highly variable, such as habitat phenology, which is itself dependent on photoperiod and temperature (Wingfield 2005, Lyon et al. 2008, Bourgault et al. 2010). A species relying on a suite of variable environmental cues to time the initiation and maturation of a stage of its annual cycle may have less flexibility than a species relying on a smaller suite or less variable cues (Both et al. 2009). Third, a species connected to a complex, multi-trophic food web may have less flexibility in its ability to respond or adapt to environmental changes than one constrained by fewer inter-specific interactions because its response to climatic changes is mediated by the responses of those species with which they are connected (Best et al. 2007, Harmon et al. 2009). Finally, climatic change that affects both the mean and frequency of critical environmental events can limit a species' flexibility by constraining its ability to respond directionally to any one change (Post et al. 2009, van de Pol et al. 2010b).

Protracted climatic changes that challenge the flexibility of a species at any of the aforementioned levels can detrimentally affect that species and cause a cascade of effects that constrain its flexibility in other portions of its annual cycle (Dawson 2008). This is especially true at the bottlenecks in the annual cycle, when a species' flexibility is inherently at its lowest (Buehler and Piersma 2008).

2) Transition points between two stages of the annual cycle are frequently those bottlenecks (Buehler and Piersma 2008). In my own study, godwit breeding success in Hudson Bay was not low because of a reduction in invertebrate abundance, a shortening of the peak of invertebrate abundance, or a dramatic shift in the timing of the peak of invertebrate abundance (Chapter 2). Instead, breeding success was compromised by the inability of godwits to complete their northward migration in time to synchronize with decreasingly predictable resource peaks in the

Hudson Bay region. Godwits breeding in Alaska have experienced a far more dramatic shift in the timing of the peak of invertebrate abundance (14 days), yet no phenological mismatch because the array of conditions on their northward route has steadily changed, allowed migrants to advance their arrival dates in line with advances in prey peaks in Alaska (Chapter 2). Bottlenecks prove to be the most vulnerable period of the annual cycle for other species as well: Red Knots that migrate through Delaware Bay and breed in the Canadian Arctic are not declining because they are starving and perishing in Delaware Bay, but likely because the poor conditions in this final northbound stopover site affect both their breeding success and annual survival by limiting the population's ability to arrive on their breeding grounds with adequate stores to quickly transition to their reproductive phase (Baker et al. 2004, Morrison et al. 2007, Vezina et al. 2012). Resident Great Tit, *Parus major*, populations are similarly not mismatched strictly because of climatic changes during the breeding season, but because those changes are coupled with climatic changes during the late winter/early spring transition period (Visser et al. 2006).

Transition points are especially inflexible because they are dependent on a set of precisely timed and contingent changes that are frequently energetically costly. First, hormonal changes that enable an individual to make the transition from one stage of the annual cycle to the next are governed by a suite of endogenous and exogenous cues that initiate the physiological, morphological, and behavioral changes necessary for each stage of the annual cycle (Wingfield 2005, Kumar et al. 2010). If a cue is not experienced or does not occur, the subsequent stage of

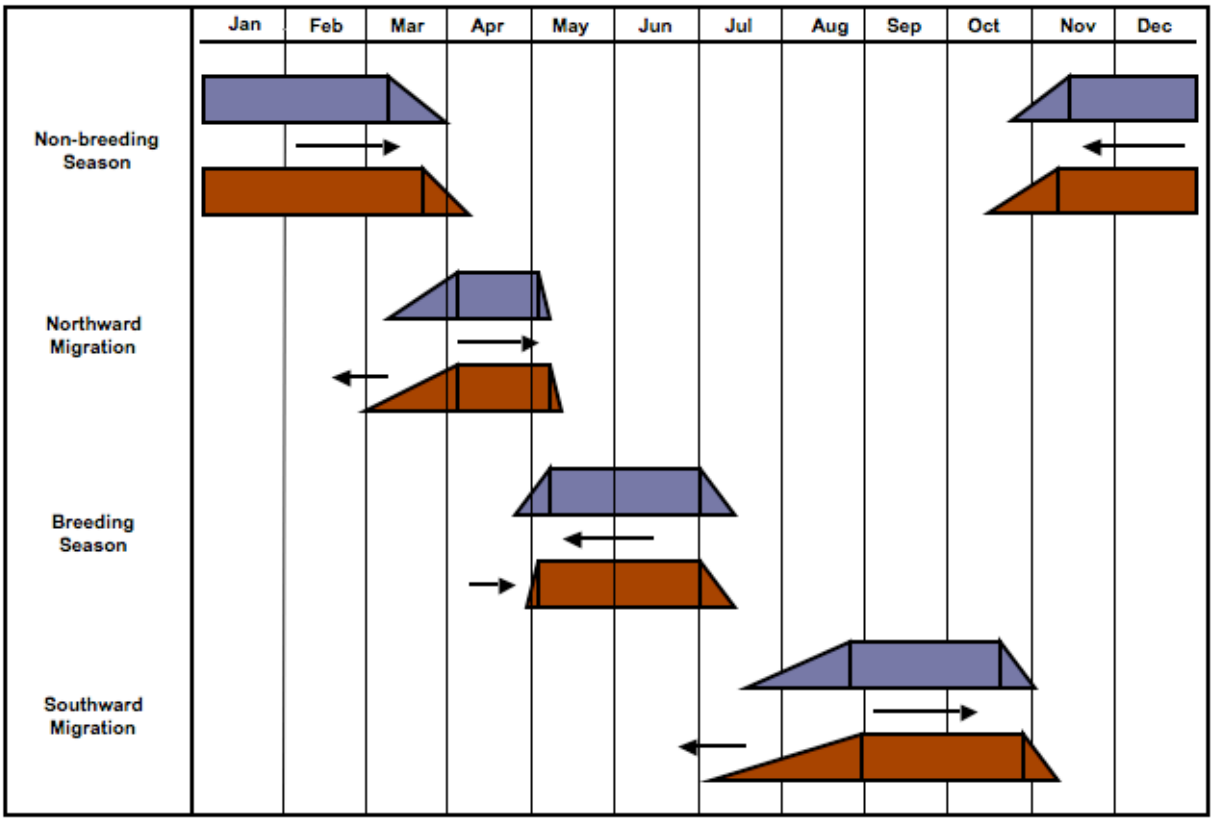

FIGURE 5.3: Organization of the annual cycle and life-history stages of Hudsonian Godwits breeding in southcentral Alaska under future climate change scenarios. The first row refers to the current organization of the annual cycle (also see Figure 5.2) and the second row refers to the alterations future climatic changes will cause to the timing of the initiation, mature, and termination phases of each life-history stage. Future climate-change related changes will cause the overlap of the mature phases of some stages. Such overlap will likely lead godwits to suffer reductions in the mature capabilities of those stages, potentially leading to reductions in breeding success and adult survival or, potentially, strong selection to alter the organization of their annual cycle.

the annual cycle may not be properly initiated or may be delayed, limiting an individual's ability to carry out that stage successfully (Dawson 2008, Gienapp et al. 2010). Second, because preparation for each new stage of the annual cycle is accompanied by a suite of energetically costly physiological, morphological, and behavioral changes, (Wingfield 2008), abbreviated preparation means that maturation of the stage also can be incomplete or delayed, with significant consequences (Bêty et al. 2003). Thus, climatic changes that alter the timing of cues or inhibit the progression of preparations during a transition phase (i.e., through reductions of food resources) can significantly delay the onset of the mature phase of a stage.

Prolonged delays in the onset or termination of a mature phase can cause the optimal timing of mature phases to overlap (Figure 5.3). When this happens, species may be unable to adequately carry out both mature phases simultaneously and an individual's performance in one or both phases can be severely reduced (Wingfield 2008). For instance, migrating godwits are incapable of overlapping their migratory and reproductive phases to a significant degree, as they are income breeders whose eggs comprise a large percentage of their lean body mass under normal reproductive conditions (Klaassen et al. 2001). Thus, unlike geese and some other species (Arzel et al. 2006), a female cannot begin developing an ovum during the final stages of its migration in order to arrive on the breeding grounds and immediately begin the onset of nest building and laying. This means that godwits are, in part, constrained by food availability on the breeding grounds in determining how quickly they can lay eggs and how synchronous they can remain with shifting phenological peaks in food resources (Chapter 2).

Climatic changes that cause mature phases to overlap may be the most obvious and fundamental way in which global climate change can disrupt the annual cycles of migratory birds. Overlapping mature phases can both lead to failures of the directly effected phases, but

also can lead to delays in subsequent stages, entailing the creation and persistence of carry-over effects (Studds and Marra 2011). Carry-over effects can lead to elevated stress levels in an individual and population, making them more susceptible to other events to which a healthy individual or population might otherwise be robust (Foley 1994).

3) Unpredictable events can, of course, alter the fate of a species or population at any point in the annual cycle, not just transition points. For instance catastrophic events can cause complete breeding failure or widespread mortality (van de Pol et al. 2010a). However, such events are less common than may be expected based on their prevalence in the literature and frequently have less severe consequences than forecasted (Smith 2011). Most populations that do succumb to catastrophic events are also likely to have been severely stressed before hand by other circumstances, such as carry-over effects (Foley 1994). Individuals that carry stress throughout their annual cycle as a result of carry-over effects chronically exist in the "emergency life-history stage" and have little flexibility to respond to additional stresses, especially catastrophic ones (Wingfield 2003). Populations that inherently have little flexibility in their annual cycle and which are having their transition phases disrupted by climatic changes are thus particularly susceptible to stochastic events.

Populations that are most stressed and thus susceptible to such catastrophic occurrences or rapid changes are often those that exist at the fringes of a species' range or the frontiers between two biomes, because such populations may inherently have the least amount of flexibility available in their annual cycle (Vargas-Rodriguez and Platt 2012). For instance, species that occupy the border between two biomes may be more likely to experience rapid shifts in their habitat than those occupying the core of a biome's range (Cobben et al. 2012). Thus, those godwit populations on the fringes — for instance godwits breeding at the northern limit of

their range in the Mackenzie River Delta of northwest Canada — may be more at risk than those in core of the species' range, as their ability to track their habitat northward is constrained both by the extent of true Arctic tundra and the immutable boundary of the Beaufort Sea (Senner 2010). Similarly, those populations inhabiting the nexus between migratory routes — for instance those connecting multiple flyways — such as those godwits breeding in extreme western Alaska, are most likely to come in contact with novel disease strains and potentially succumb to a disease epidemic (Ramey et al. 2010).

PROGNOSES

Taking into account these three basic tenets — flexibility, transition points, and stochastic events — the prognoses for all three godwit populations share some commonalities. Most important, all three populations migrate the length of the Western Hemisphere and intersperse multi-day, non-stop flights with stops at traditional staging areas where they rest and refuel for subsequent flights. While such a pattern is superficially similar to that of many other migratory birds, the distances involved and the levels of physiological stress incurred may be orders of magnitude above those experienced by the majority of migratory birds (Warnock 2010, Piersma 2011). As such, changes in food availability or wind regimes may not only alter their migration strategy — potentially causing individuals to make use of additional stopover sites — but may cause the complete collapse of the godwit annual cycle (Baker et al. 2004, Dey et al. 2011). Broad-scale changes to midcontinental wetlands and the increased incidence of hurricanes in the North Atlantic, if experienced at the level projected by the most extreme predictions, indeed appear to have the potential to disrupt the godwit annual cycle permanently (Johnson et al. 2010, Villarini and Vecchi 2012).

Catastrophic failure, however, is unlikely for Hudsonian Godwits as a species, at least in the near term. Instead, climatic changes projected for the coming century portend different responses by each of the three main breeding populations (Table 5.1). Because godwits breeding in Hudson Bay are already mismatched with local resource phenology (Chapter 2), their transition into the breeding season is currently the most critical component of their annual cycle. Shorebirds are largely income breeders (Klaassen et al. 2001), although in some cases they may be able to deposit resources acquired during migration in their eggs (Morrison and Hobson 2004). Individuals that arrive at breeding sites with greater reserves have higher survivorship (Morrison et al. 2007), but also may have higher breeding success through the influence of reserves on an individual's ability to transition their physiology quickly to breeding readiness and on subsequent nest incubation behavior (Smith et al. 2007, Vezina et al. 2012). Therefore, preparation for northward migration, successful migratory flights, and productive stopovers that enable rapid northward movement are paramount for Hudson Bay godwits, as these will allow them to arrive at breeding sites quickly and in the best possible condition for the breeding season. Climatic changes that alter food availability on the non-breeding grounds and during northward migration and extreme weather during long migratory flights are the most likely factors to affect the stability of this godwit population. Current climate projections suggest that continued changes to these parts of the annual cycle, such as wetland drying in the Prairie Pothole Region and increasing mid-continental winds, are highly probable (Cook et al. 2008, Johnson et al. 2010) and cast further doubt on the future status of the Hudson Bay population.

Godwits breeding in Alaska currently are not experiencing a mismatch and have buffer events in their annual cycle that erase accumulated stress, allowing them to move between stages of their annual cycle free of carry-over effects (Chapter 1, Chapter 3). Their current status could

be eroded if changes in habitat and food availability cause accumulating stress that carries over between stages of the annual cycle. Post-breeding staging sites in central Saskatchewan exist at a critical transition point between the rapid sub-Arctic breeding season and the long southward migration. During this transition, godwits are overcoming stress from the breeding season and northward migration, initiating prebasic molt, and fueling for a non-stop flight to the Amazon Basin of Colómbia (Piersma et al. 2003, Walker et al. 2011, Chapter 3). These central Saskatchewan staging sites may experience substantial drying in the next century, casting in doubt their ability to continue to serve as buffer event sites for this population (Johnson et al. 2010). Likewise, staging sites in the central U.S. during northward migration, which could also be degraded by wetland drying, would alter the stress load carried by godwits into the breeding season (Morrison et al. 2007). Given the flexibility that they have already exhibited, which stems from the reliability and simplicity of the cues used to time their arrival at their breeding sites (Chapter 1), the overall outlook for coastal Alaskan godwits is the most positive of any of the three breeding populations.

The little-studied godwits breeding in northwest Canada and northeastern Alaska may be experiencing a phenological mismatch similar to the Hudson Bay godwits, both because of their shared migration timing and because these northernmost breeding grounds are undergoing some of the most rapid summer warming on the planet (Hinzman et al. 2005). As for the Hudson Bay population, any changes in food and habitat availability during the non-breeding season and northward migration would have large effects on the population's annual cycle. However, habitat loss through the migration of woody vegetation onto the Arctic coastal plain may overwhelm other climate change-related challenges and rapidly endanger this population (Virkkala et al. 2008).

TABLE 5.1: Likelihood of potential climate related changes detrimentally affecting stages of the annual cycle of Hudsonian Godwits. A) refers to the southcentral and western Alaska breeding population; HB) refers to the Hudson Bay breeding population; and NT) refers to the Northwest Territories and northeastern Alaska breeding population.

Annual Cycle Stage	**Phenological**	**Species Distribution**	**Disease Risk**	**Food Avail.**	**Extreme Weather**	**Habitat Avail.**
Non-breeding Season	**A)** Unlikely	Unlikely	Unlikely	Possible	Unlikely	**Probable**
	HB) Unlikely	Unlikely	Unlikely	Possible	Unlikely	**Possible**
	NT) Unlikely	Unlikely	Unlikely	Possible	Unlikely	**Possible**
Northward Migration	**A) Possible**	Unlikely	Possible	Probable	Probable	Probable
	HB) Occurring	Unlikely	Possible	Probable	Probable	Probable
	NT) Occurring?	Unlikely	Possible	Probable	Probable	Probable
Breeding Season	**A) Possible**	Unlikely	**Possible**	**Possible**	**Unlikely**	**Possible**
	HB) Occurring	Unlikely	**Unlikely**	**Probable**	**Possible**	**Probable**
	NT) Occurring?	Unlikely	**Unlikely**	**Probable**	**Possible**	**Probable**
Southward Migration	**A)** Unlikely	Unlikely	**Possible**	**Probable**	Occurring	**Probable**
	HB) Unlikely	Unlikely	**Unlikely**	**Unlikely**	Occurring	**Possible**
	NT) Unlikely	Unlikely	**Unlikely?**	**Probable**	Occurring	**Probable**

CONCLUSION

Identifying the points that currently limit a species' annual cycle is key to understanding those climatic changes that will most affect their ability to reproduce and survive (Figure 5.3). This means understanding the underlying flexibility existing within their annual cycle and the degree to which climatic changes could compromise that flexibility and lead to overlapping mature phases. For species vulnerable to phenological mismatches, this means understanding the phenological regimes currently experienced by the species, especially during the period immediately preceding the breeding season, and identifying those cues relied upon to time the initiation of breeding efforts (Lyon et al. 2008, Chapter 2). For those species not likely to be affected by phenological mismatches, it means identifying those habitats and food resources that allow them to transition between stressful parts of the annual cycle and understanding how those may be affected by climate change (Buehler and Piersma 2008, Chapter 3). For species that are already severely stressed, it means understanding how stochastic events caused by climate change may compound their other problems (Smith 2011, Chapter 4).

Establishing a common framework for the study of the effects of climate change on migratory birds is critical for making projections about future population dynamics and conservation priorities. The organism-environment framework for understanding a species' entire annual cycle approaches climate change at the necessary scales — from the mechanistic to the global. With such a framework in hand, scientists and conservationists can hopefully make more precise and accurate assessments of those species in imminent danger.

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